Chapter 11:
Biological Diversity in Lentic Riparian Ecosystems

Introduction

Rationale and Objectives

This study of biological diversity in lentic riparian ecosystems was intended to complement the study of lotic riparian ecosystems. Lentic ecosystems provide important habitat for amphibians, reptiles, and aquatic, riparian, and meadow birds in the Sierra Nevada, and many animals in the basin, such as waterfowl and amphibians, use primarily lentic habitats. Every species of amphibian in the Lake Tahoe area is known to breed in lakes or wet meadows, at least occasionally (Stebbins 1985). Many waterfowl and shorebirds in the basin breed or forage at lakes (Orr and Moffitt 1971).

Lentic ecosystems in the Lake Tahoe basin have undergone significant alteration by humans in recent decades and their integrity is of concern (Manley et al. 2000). Lakes are a primary focus of recreational activities in the basin, including boating, camping, and fishing. Several lakes in the basin have been dammed, while many small ponds have been drained. Much of the marshland on the south shore of Lake Tahoe has been developed for housing and businesses. Nonnative trout have been introduced into nearly all aquatic ecosystems in the basin (Elliott-Fisk et al. 1997); many lakes continue to be stocked yearly by the California Department of Fish and Game. Introduced bullfrogs have spread through most of the south shore's marshes and now occupy several lakes around the south shore. Many wet meadows are subject to livestock grazing. Very few lentic ecosystems in the basin have escaped human alteration; only a few off-trail lakes without exotic fish in Desolation Wilderness, the Upper Truckee watershed, and the Mt. Rose Wilderness may currently be considered pristine.

The primary goal of this study of lentic ecosystems was to describe environmental correlates of bird, amphibian, reptile, and littoral zone plant alpha diversity at lakes and wet meadows in the basin. (Single-species relationships are treated in Chapter 12.) Alpha diversity is the number of distinct taxa in a given location (Primack 1993) and is the primary measure of biological diversity used here (see Chapter 1). We measure alpha diversity as the species richness of different taxa, supplemented by information on the abundance of individuals. We also examined gradients of habitat features in addition to the richness and abundance of these species groups. Our data also provide baseline information on occurrence of animals and plants at locations throughout the basin to which future survey results may be compared. Understanding environmental relationships of amphibian, reptile, bird, and littoral zone plant alpha diversity in the basin can provide a foundation for predicting which areas are likely to support high species richness and for identifying restoration opportunities.

This study of lentic ecosystems in the basin included large lakes, ephemeral and permanent ponds, reservoirs, wet meadows, and sewage ponds. The range of lentic ecosystems represents a continuum rather than discrete types. Lentic ecosystems are often classified into different types (e.g., Moyle 1996); however, different types might serve similar ecological roles for some species groups. As such, we sampled all lentic types using the same general methodology and did not differentiate among them in our analyses. This treatment facilitated identifying a broad range of habitat features available to the taxonomic groups of interest. Individual water bodies of each type are referred to as "lentic units" in this document.

Birds

Environmental Correlates of Alpha Diversity

We expect that environmental characteristics that are useful for predicting the biological diversity of birds will vary by the species' habitat associations. Specifically, characteristics of the lentic units, such as area and substrate, will be better predictors of the diversity of aquatic-, riparian-, and meadow-associated (ARM) birds than of the diversity of upland birds. Upland birds are more likely than ARM birds to be influenced by habitat features, such as terrestrial vegetation, that describe the areas upland birds primarily occupy.

Environmental factors that may affect ARM bird distribution include elevation, habitat size, human disturbance, vegetative diversity and abundance, and food availability (Cooperrider 1986, Baldassarre and Bolen 1994). A negative relationship between species richness and altitude has been shown repeatedly in ecological studies (Begon et al. 1990); in addition, oligotrophic lakes, typical of high elevations, have low primary productivity (Odum 1971) and are likely to support a lower diversity of ARM birds. At higher elevations, food resources, particularly vegetation and abundance of macroinvertebrates, are limited by the nutrient-poor conditions, and given the strong association of ARM bird occurrence with food availability (Murkin and Kadlec 1986, Owen and Black 1990), a greater diversity of these birds can be expected at lower elevations, where food resources are presumably richer.

The areal extent of aquatic and riparian ecosystems can affect bird diversity, but few studies have addressed this relationship (Baldassarre and Bolen 1994). For most biota, the greater the area sampled, the more species encountered (Rosenzweig 1995). For example, bird species richness has been found to increase with habitat size for marshlands (Brown and Dinsmore 1986). We expect that the species richness of all bird groups will increase with the size of lakes, ponds, and wet meadows. Because larger sample units require more sampling, which is likely to detect more species, the effect of increased sampling must be accounted for. We expect that when species richness is considered per unit of survey effort, a positive relationship between richness and area may not be observed.

Bird species richness and abundance are typically closely tied to food availability. Waterfowl feed on both aquatic vegetation and macroinvertebrates; caddisflies (Tricoptera) and mayflies (Ephemeroptera) are among the more visible invertebrates important for waterfowl (Eldridge 1990). Shorebirds and riparian- and meadow-associated passerines are primarily invertivores as well (Ehrlich et al. 1988). Availability of vegetative forage and macroinvertebrates should therefore be important predictors of aquatic and riparian–meadow bird occurrence. Several studies have linked ARM bird distribution to macroinvertebrate densities in marshlands (Joyner 1980, Murkin and Kadlec 1986, Colwell and Landrum 1993, Safran et al. 1997) and substrate has been used to predict shorebird occurrence through its relationship to macroinvertebrate density (Yates et al. 1993).

Human Disturbance

Human disturbance can dramatically affect vertebrate abundance (Cooperrider 1986). Many forms of disturbance occur in the basin (e.g., development, human visitation, presence of dogs) and may affect ARM bird occurrence directly (e.g., by causing abandonment of nests [Knight and Cole 1995]) or indirectly (e.g., by causing increased nest predation [Mikola et al. 1994]). Human disturbance has been shown to be negatively associated with occurrence and abundance of some shorebirds (e.g., Pfister et al. 1992) and waterfowl (e.g., Mikola et al. 1994). Thus, we would expect ARM birds to occur more frequently in pristine sample units than in disturbed sample units. However, in the Lake Tahoe basin, disturbance and elevation are inversely related, so it may be difficult to separate their effects.

Concern for ARM bird populations has grown with the increasing awareness of the effects of wetland development on birds. In the Lake Tahoe basin, a great majority of marshes extant before Euroamerican settlement have been developed and many lakes have been altered (Manley et al. 2000), prompting concerns about ARM birds' abilities to adapt to such intense disturbance.

Amphibians

Despite popular attention and many survey efforts in the Sierra Nevada (e.g., Drost and Fellers 1996, Knapp and Matthews 2000) little is known about the status of amphibians in the Lake Tahoe basin, apart from some information on species composition. Most information on the distributions of the less common amphibians, such as the mountain yellow-legged frog, has consisted of anecdotal sightings; more systematic surveys have not been performed in the basin until very recently. S. Lehr (pers. comm.) and K. Leyse (pers. comm.) surveyed several sites on the east side of Desolation Wilderness in 1997-2000. Panik and Barrett (1994) surveyed 2 sites in the basin along the Truckee River but detected no amphibians. Extensive surveys using standard protocols have been lacking in the basin while the urgency of performing such surveys grows. Knowledge of the diversity patterns, distributions, and habitat relationships of the basin's amphibians is vital for their management.

Environmental Correlates of Alpha Diversity

Studies of amphibian diversity have generally been confined to species-rich areas such as the tropics, subtropics, and Pacific Northwest, where there exists a variety of terrestrial as well as aquatic species (see, for example, Duellman and Trueb 1986, studies in USDA 1991b, Pearman 1997). Composite measures of amphibian diversity, such as species richness, may not be especially sensitive measures of favorable habitat conditions for amphibians in the basin because of the small number of species and their diverse habitat associations. Little is known about environmental correlates of amphibian species richness in species-poor regions like the basin.

Studies of amphibian species richness from other areas may not prove useful for comparison. Most comparative studies of amphibian species richness have examined differences in species richness in large areas (e.g., using data from different countries), and have focused on terrestrial species. Few studies on local variations in aquatic amphibian species richness in temperate latitudes have taken place. Amphibian species richness has been shown to decline over long gradients of elevation (Duellman and Trueb 1986) and richness increases with increasing rainfall (Duellman and Trueb 1986). However, these patterns would not be expected in the basin, where precipitation increases with elevation and falls primarily as snow. Furthermore, the basin may be at too high an elevation, may represent too short a gradient, and may contain too few species to observe significant changes in amphibian species richness. Studies in relatively species-rich lentic ecosystems in Ontario have found that species richness is lower in the presence of predatory fish (Hecnar and McCloskey 1997) and that water chemistry is a poor predictor of species richness (Hecnar and McCloskey 1996). It is unknown if these factors influence amphibian diversity in the basin.

Human Disturbance and Amphibian Decline

The worldwide decline of amphibians is now a common topic in the scientific and popular literature (e.g., Hayes and Jennings 1986, Barinaga 1990, Blaustein and Wake 1990, Phillips 1990, Knapp and Matthews 2000). Hypothesized reasons for amphibian decline are varied; proposed causes include habitat destruction, introduced species, increased exposure to ultraviolet light, pesticides, and drought (Hayes and Jennings 1986, Jennings 1996, Drost and Fellers 1996). Very likely, causes of decline vary by region and by species; while introduced trout might be the main cause of decline of the mountain yellow-legged frog (Bradford et al. 1993, Knapp and Matthews 2000), habitat destruction, overharvesting, and introduced bullfrogs are probably the cause of the decline of the California red-legged frog (*R. aurora draytonii*; Moyle 1973, Hayes and Jennings 1986). Determination of the causes of amphibian decline must begin with an understanding of habitat relationships and an assessment of baseline conditions.

Littoral Zone Plants

The distinction between aquatic plants and terrestrial plants is necessarily inexact (Prescott 1969, Riemer 1984), as changes in the boundaries of lentic ecosystems throughout the year due to drying mean that plants may be found in water for portions of the year only. Aquatic plants can generally be defined as "plant[s] that [are] normally found in nature growing in association with free-standing water whose level is at or above the surface of the soil" (Riemer 1984). Thus defined, they include floating unattached plants (e.g., duckweed), floating attached plants (e.g., water lilies), emergent plants (e.g., sedges and rushes), and submergent plants (e.g., watermilfoil; Riemer 1984). In this study, we assess plants known to be aquatic and those that are inundated for part of the growing season (e.g., lodgepole pine, *Pinus contorta*, and willows, *Salix* spp.), and refer to them as littoral zone plants.

The littoral zone plants of the basin have not been the focus of any ecological studies, although they have been inventoried as part of an extensive floral treatment of the basin by Smith (1973, 1983). In addition, some site-specific studies have been conducted that included surveys of aquatic vegetation (e.g., at Grass Lake: Stewart 1978, Burke 1987). More recently, a list of all vascular plants known to occur and potentially occurring in the basin was compiled (Holst and Ferguson 2000). The distribution, species diversity, and ecological relationships of the basin's littoral zone plants remain poorly known.

Plants are important components of aquatic ecosystems, and their richness and abundance may influence the occurrence of other species such as birds and amphibians. Plant species richness has also been shown to be an indicator of pollution; over many years, changes in species richness can indicate eutrophication, siltation, and other pollution (Hill 1997). Thus, our reasons for surveying littoral zone plants were twofold: to describe patterns of their alpha diversity and to describe them as habitat features for other species. We focused our efforts on overall patterns of plant diversity and frequency, and did not investigate the ecological relationships of individual plant species.

Environmental Correlates of Alpha Diversity

Factors affecting the distribution and diversity of littoral zone plants can include water depth, water chemistry, substrate, and area of habitat. Aquatic macrophytes generally grow in shallow water (Goldman and Horne 1983); thus, surveys in the littoral zone of large lakes are likely to detect the majority of aquatic macrophytes. Various aspects of water chemistry are known to affect aquatic plants, including dissolved oxygen, pH, temperature, and nutrient availability (Riemer 1984, Lewis and Wang 1997). Extremes of any of these parameters can be detrimental to plant growth and species diversity. For example, decreased pH due to acid rain has been shown to damage plant tissue and change species composition (Lewis and Wang 1997). Substrate is another important factor in littoral zone plant distribution; certain substrates are more conducive than others to the growth of aquatic macrophytes. Silt or sand substrates facilitate macrophyte rooting, while rocky substrates are better environments for algae (Goldman and Horne 1983). The species richness of aquatic plants also has been shown to increase with habitat area (Weiher and Boylen 1994). However, because larger areas require more sampling, thus permitting the detection of more species, this relationship may not be observed on a per unit area basis.

Human Disturbance

Aquatic plants are likely to have been significantly affected by disturbance to aquatic ecosystems in the basin. Modifications of lake and pond substrates through excess siltation, changes in water chemistry brought about by atmospheric deposition, and direct impacts such as grazing and recreation undoubtedly have affected the distribution and diversity of littoral zone plants. Studies such as ours that document environmental conditions related to littoral zone plant diversity and baseline conditions at sampled sites should be of use in assisting the preservation of these often-ignored components of the basin's aquatic ecosystems.

Organization of the Chapter

The organization of the chapter is described here to help orient the reader. The study area is described earlier in Chapter 2; the methods for the lentic study appear below. Results are presented in sections starting with the environmental characteristics of the basin, followed by analyses of alpha diversity of birds, amphibians and reptiles, and littoral zone plants. We conclude with discussions of each section of results and their conservation and management implications and a summary discussion that compares results across taxonomic groups.

METHODS

We surveyed 88 lentic sample units in 1997 and 1998: 72 lakes and 16 wet meadows. Methods of sample unit selection, data collection, and data analysis are described below.

Sample Unit Selection

Lakes

The Lake Tahoe basin contains over 300 lakes. We took the following approach to select lakes for sampling.

Stratification

We identified 4 gradients as the primary features affecting lake habitat conditions in the Lake Tahoe basin: elevation, orientation to Lake Tahoe, lake size, and disturbance. We chose a representative sample of lakes along all 4 gradients.

Lakes were assigned to one of two elevation classes (low and high). Elevations of lakes ranged from 1900 m to 2817 m. The mean and median lake elevation were both approximately 2290 m. We assigned lakes located at < 2290 m in elevation to the "low" elevation class and lakes located at ≥ 2290 m in elevation to the "high" elevation class.

Basin orientations reflected differences in ranges in temperatures and precipitation resulting from elevation gradients and climate patterns (Fig. 74). The west side of the basin is mostly influenced by coastal climate patterns, while the east side is mostly influenced by continental climates typical of the Great Basin. Watersheds on the west side have greater elevation ranges and higher average precipitation than watersheds on the east side. The north and south sides are transitional zones in terms of elevation gradients and precipitation clines. We used the north–south range line N 18 E, which runs approximately through the center of Lake Tahoe, to delineate two basin orientations: west side and east side. Lakes west of N 18 E were classified as west side, while lakes east of N 18 E were classified as east side.

Lakes were assigned to one of 3 size classes. Lake sizes ranged widely, from 0.1 ac (0.03 ha) to 1410.2 ac (570.9 ha) and had a Poisson distribution, with over 150 lakes being smaller than 1 acre (0.4 ha), and only 3 lakes being larger than 100 acres (40 ha). We created a frequency histogram using a log scale to differentiate 3 size classes: small (0 to 1 ac), medium (>1 to 10 ac), and large (>10 ac).

We determined disturbance classes from a Recreation Opportunity Spectrum map (USDA 1988), which identified 5 levels of development in the basin: urban, rural, roaded natural, semi-primitive motorized, and semi-primitive non-motorized (Appendix 2). Based on the ROS levels, we created 3 disturbance classes: high (urban–rural), moderate (roaded natural–semi-primitive motorized), and low (semi-primitive non-motorized).

Selection

Stratification by elevation, orientation, and size resulted in 12 elevation–orientation–size classes. Time and money constraints dictated a sample size of 48 lakes in 1997 and 24 lakes in 1998. We randomly chose 4 lakes within each of the 12 classes for a total of 48 lakes in 1997 and 2 additional lakes per class for a total of 24 lakes in 1998. Sample lakes were located at least 500 m apart to ensure independence of bird point counts (below). We included all 3 lakes greater than 100 ac in the 1997 sample to ensure adequate representation of large lakes in the sample. Selected lakes were then post-stratified by disturbance in both years. We dropped lakes in overrepresented disturbance classes and randomly chose lakes in underrepresented disturbance classes as replacements if the distribution of lakes relative to disturbance was not relatively equivalent by elevation, orientation, or size. Disturbance and elevation are inversely related within the basin, so the distribution of disturbance levels across elevation is less than perfect. We found that several randomly selected lakes were no longer in existence (e.g., due to being drained) or were otherwise inaccessible (e.g., due to private ownership). We selected the nearest surveyable lake in the same elevation–orientation–size class when we could not survey a randomly selected lake.

The 72 sample lakes were fairly evenly distributed across elevation, orientation, and size classes and represented varying degrees of disturbance (Table 180, Appendix 20). The sampled lakes represented a wide range of disturbance, including several off-trail backcountry sample units with relatively little human visitation (e.g., Lagomorph Lake, Pond of the Woods, and Summit View Lake), many sample units with moderate use (e.g., Bliss Pond, Susie Lake, and Lost Lake) several heavily used recreational and urban sample units (e.g., Lake Baron, Tallac Lagoon, and Watson Lake), 2 sewage ponds (Round Hill and Sweetwater), 1 storm runoff basin (Wildwood Basin), and 3 lakes on golf courses (Birdie Pond, Divot Pond, and Edgewood Lake). Many were human-altered, for example by dams (e.g., Burton Pond, Dammed Pond, Marlette Lake, Spooner Lake) or by restoration (Seneca Pond). Sampled lakes were located throughout the basin (FIG.). We refer to sample units by their names according to USGS 1:24,000 topographic maps or local custom. Unnamed sample units were assigned names.

TABLE 180. Lake selections and their characteristics based on 4 gradients: orientation, elevation, size, and disturbance. Lakes were surveyed in 1997 and 1998 in the Lake Tahoe basin.

Orientation	East						West						
Elevation	High			Low			High			Low			
Size	S	M	L	S	M	L	S	M	L	S	M	L	TOTAL
Low Dist	4	5	4	0	1	1	3	4	4	1	1	2	30
Mod Dist	2	0	2	2	2	1	2	2	1	4	5	1	24
High Dist	0	1	0	4	3	4	1	0	1	1	0	3	18
TOTAL	6	6	6	6	6	6	6	6	6	6	6	6	72

Wet meadows

The population of meadows in the basin was defined by including wet meadows depicted on USGS 1:24,000 topographic maps (as indicated by marsh–swamp–muskeg icons) combined with "moist meadow" and "wet meadow" designations from a map of riparian areas derived from professional interpretation of 1:30,000 infrared aerial photographs of the basin from 1987 (USGS 1994). We used the following approach to identify meadows for sampling in 1998.

Stratification

We used square-mile sections to identify meadows for sampling because no complete database of the basin's meadows was available. We stratified all square-mile sections in the basin by orientation and elevation. Sections were stratified along these gradients in the same manner as were lakes (above), resulting in 4 orientation–elevation classes. Meadows were not stratified by size or disturbance class because of the small number of meadows to be sampled compared to lakes.

Selection

We randomly chose 4 sections within each orientation–elevation class for a total of 16 sections and selected for sampling the wet meadow closest to the center of each selected section. As with lakes, meadows were located at least 500 m apart. Selected meadows that were too close to sampled lakes were dropped and replaced with the meadow next closest to the center of the selected section. Field reconnaissance was necessary to confirm that selected meadows were suitable for amphibian breeding (i.e., having no standing water at least 2 cm deep). Meadows determined to be unsuitable were dropped and the next closest meadow to the center of the section was selected.

The 16 sample meadows (Fig. 74) were relatively evenly distributed across elevation and orientation classes (Appendix 20). They ranged in size from less than half a hectare to over 11 hectares. Most appeared to have low disturbance, although a few were near hiking trails or roads.

FIG. 74. Names, locations, and basin orientations of lentic sample units surveyed in 1997 and 1998 in the Lake Tahoe basin.

Data Collection and Summaries

Data collection at each sample unit consisted of surveys to describe bird species composition and abundance, amphibian and reptile species composition and relative abundance, littoral zone plant species composition and relative abundance, and habitat features (Figs. 75 & 76). We characterized the bird community using point count surveys and described amphibian, reptile, and littoral zone plant communities by surveying the perimeters of lakes and the entirety of wet meadows. Across all protocols, low elevation sample units were sampled earlier in the season, as they were accessible earlier than high-elevation sample units and generally had earlier bird, amphibian, and reptile breeding seasons. Six observers surveyed lentic sample units in 1997 and 1998 (Appendix 21).

Bird Surveys

We conducted point count surveys to describe the species composition and abundance of birds. Pacific treefrog and Douglas squirrel vocalizations also were recorded during point counts. Ralph et al. (1993) recommended that point counts be located a minimum of 250 m apart; given the open environment associated with many lentic units, we established count stations 500 m apart around the perimeter of each sample unit to ensure point counts were independent (Figs. 75 & 76). Count stations at sample units with multiple counts were located by conducting the first count and then pacing the distance along the perimeter until the straight-line distance between points was approximately 500 m. If visibility was limited at the designated count location, the observer moved to the closest point with good visibility.

Point counts were performed between 0530 and 0930 hrs, beginning no sooner than 15 min after sunrise. Each point count lasted exactly 20 min, with data separated into 10 min increments. The observer stood at a station and recorded every bird seen or heard at any distance (including birds flying overhead). Observers used binoculars to aid in identifying birds seen at a distance. If more than 1 observer surveyed a sample unit at the same time (primarily at larger sample units), observers were located at different stations and counts occurred simultaneously. An absolute number of birds present at the sample unit for all counts combined was derived by comparing of all individual counts and omitting individual birds counted more than once.

Bird alpha diversity was represented by measures of species richness and abundance. Only native species were included in calculations. Bird species richness and abundance were each calculated as an average across all point counts at each sample unit, so as to exclude from consideration the increased sampling effort at some sample units. We also calculated the total species richness (“site bird diversity”) and total abundance across all point counts at each sample unit.

Bird species richness and abundance were also calculated for each of 3 habitat groups: aquatic, riparian–meadow, and upland. Birds were considered aquatic if they were obligately aquatic for some behavior, such as breeding or foraging. Aquatic birds included loons, grebes, herons, egrets, bitterns, swans, geese, ducks, rails, plovers, shorebirds, terns, dippers, and kingfishers (cf. Colwell and Dodd 1995). Birds were considered riparian–meadow associates if they primarily occupied riparian or meadow areas (Ehrlich et al. 1988). Riparian–meadow birds included some flycatchers, swallows, some wrens, blackbirds, some sparrows, and some warblers. The remainder of the bird fauna was considered associated with upland ecosystems.

Amphibian and Reptile Surveys

Amphibian and reptile surveys and bird surveys were conducted no more than 7 days apart so that the surveys described conditions at roughly the same point in time. Amphibian and reptile surveys were conducted between 1000 and 1700 hrs. We surveyed amphibians and reptiles at lakes by walking the entire perimeter (Fig. 75). If 2 observers were present at a lake (multiple observers generally were present at the larger sample units), they began at the same point and surveyed in opposite directions until they met. If more than 2 observers surveyed a lake, they began at predetermined points and surveyed until they reached the adjacent observer's starting point. Lake perimeters were treated as a 10 m wide transect, with 5 m surveyed on either side of the shoreline (Fig. 75). Amphibians and reptiles outside this 10 m wide transect that were detected during the survey were also recorded.

We surveyed amphibians and reptiles at wet meadows by walking in a zig-zag fashion through each meadow (Fig. 76). When we encountered standing water too deep to walk through, we walked the perimeter of the standing water. If multiple observers surveyed a meadow, the meadow was divided among the observers so that the entire meadow was covered. At all sample units, observers spent approximately 15 min searching per 100 m walked. Observers spent most of the time walking in the water, searching through emergent vegetation with a long-handled dip-net and overturning rocks, logs, and debris to reveal amphibians and reptiles (Fellers and Freel 1995). All amphibian and reptile species seen or heard were recorded, identifying species, life stage, and number of individuals. Observers listed all adults and subadults individually and tallied individual larvae and egg masses using abundance classes (1 to 3, 4 to 10, 11 to 50, 51 to 100, 101 to 250, 250 to 500, and >500).

Amphibian alpha diversity was represented by native amphibian species richness, calculated as the number of native species observed per sample unit. The total abundance of amphibians was not calculated because counts of individuals of different life stages cannot be combined given the varying survivorship among age classes for most amphibians (Duellman and Trueb 1986). Further, for amphibians with few detections, distinguishing between low abundance and high abundance runs the risk of being arbitrary.

Littoral Zone Plant Surveys

We identified plants as littoral zone associates if they were rooted underwater or if they were unattached and floating on the surface. We did not distinguish among floating plants, emergent plants, and submergent plants, but rather included all littoral zone macrophytes (vascular plants, mosses, and liverworts) in calculations of diversity. Surveys for diatoms and algae were beyond the scope of this study.

Littoral zone plants were surveyed by conducting 50 to 73 transects at each sample unit. At lakes, we determined transect locations according to timed intervals or by paced distance, aiming for a minimum of 50 transects per lake. At meadows, we randomly determined a starting point for a straight line across the longest dimension of the meadow. We walked from that point to the opposite end of the meadow, determining transect starting points by pacing the distance between points to ensure at least 50 transects were conducted per meadow. If some portion of the sample unit remained to be surveyed once 50 transects were conducted, observers continued conducting transects at the same distances or timed intervals. At all sample units, we recorded the presence of littoral zone plant species intersected by a 3-m transect line perpendicular to the shore at lakes (Fig. 75) or along a randomly-determined compass bearing from the observer’s position in meadows (Fig. 76). Plants unknown to the observers were collected for later identification.

Two measures of alpha diversity were generated. Littoral zone plant diversity was defined as the mean number of plant taxa per transect. Littoral zone plant frequency was defined as the proportion of transects per sample unit containing plants of any species.

Environmental Characteristics

We described abiotic and biotic habitat features relevant to birds, amphibians, reptiles, and littoral zone plants. Habitat features consisted of 4 groups: abiotic environmental characteristics, sample unit characteristics, vegetation characteristics, and other biota (Table 181).

We described vegetation and percent slope at 2 scales, depending on the species group of interest. A 200 m radius around each sample unit was chosen as an appropriate scale within which to describe environmental variables for birds because it is slightly larger than the distance at which most birds are detected using point counts (Ralph et al. 1993). A 50 m radius was chosen for plants, amphibians, and reptiles because individuals in these groups detected during surveys at each unit would spend most or all of their time within this distance, and it represents a reasonable zone of influence for these species.

Some environmental variables were transformed to make their distributions approximate normality (Table 181). We used the following 3 transformations: log-normal, square root, and arcsine of square root (Sokal and Rohlf 1981). Log-normal transformations were applied as the natural log of the variable or the natural log of the variable plus 1 for variables with some zero values (Sokal and Rohlf 1981). Transformations were not applied when variables were already normally distributed or when transformations were unhelpful in approximating normality.

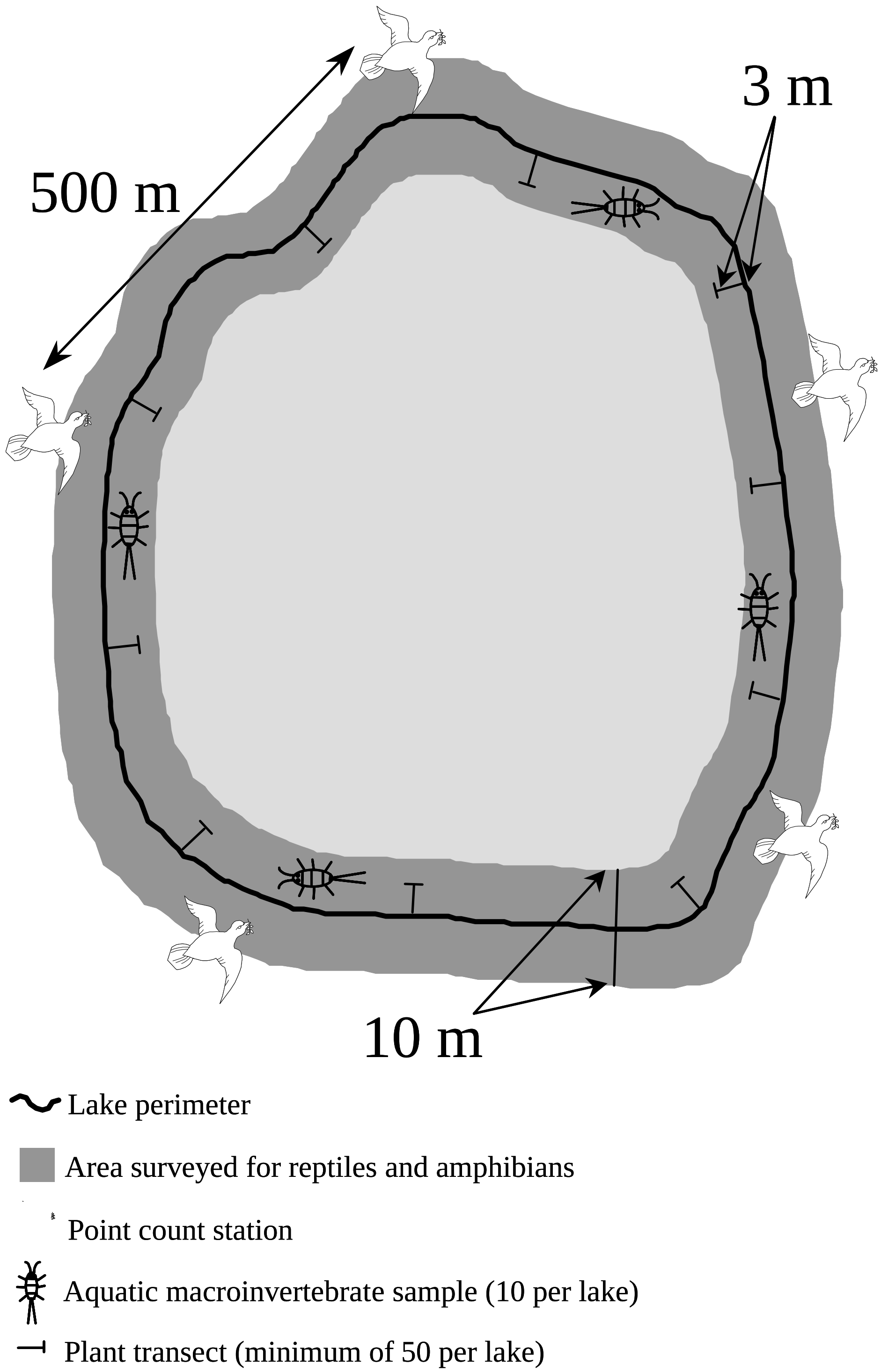


FIG. 75. Schematic of biological sampling conducted at each lake sampled in the Lake Tahoe basin.

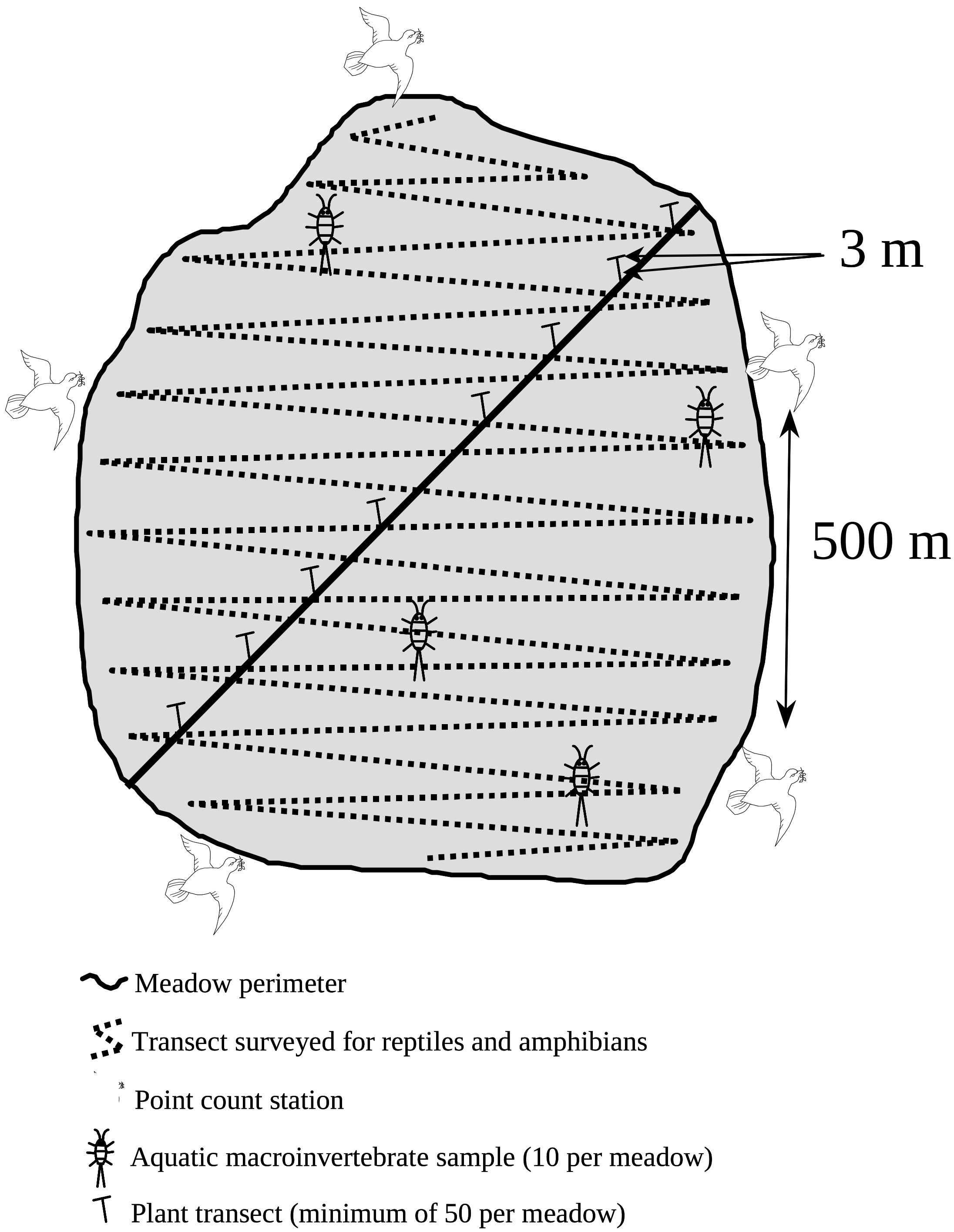


FIG. 76. Schematic of biological sampling at wet meadows in the Lake Tahoe basin.

TABLE 181. Environmental variables described for 88 lentic sample units in the Lake Tahoe basin. Transformations applied are indicated, where x = the untransformed variable. Dashes indicate no transformation was used.

Environmental variable	Metric	Transformation
Abiotic environmental characteristics:		
Elevation	m	$\sqrt{x}$
Mean annual precipitation	cm	-
Orientation to Lake Tahoe	east, west, north, south	-
Percent slope	avg. within 50 and 200 m	-
Sample unit characteristics:		
Area	ha	$\ln x$
Perimeter	m	$\ln x$
Depth	m	$\ln x$
Bedrock	proportion of transects	arcsine ($\sqrt{x}$)
Boulders	proportion of transects	$\sqrt{x}$
Cobbles	proportion of transects	$\sqrt{x}$
Pebbles	proportion of transects	arcsine ($\sqrt{x}$)
Sand	proportion of transects	$\sqrt{x}$
Silt	proportion of transects	arcsine ($\sqrt{x}$)
Vegetation characteristics:		
Littoral zone plant frequency	prop. of transects with plants	arcsine ($\sqrt{x}$)
Littoral zone plant diversity	mean # plant taxa/transect	$\sqrt{x}$
Floating and submerged log frequency	proportion of transects	$\sqrt{x}$
Overhanging vegetation frequency	proportion of transects	$\sqrt{x}$
Aspen	prop. area within 50 & 200 m	-
Meadow	prop. area within 50 & 200 m	$\sqrt{x}$
Mixed conifer	prop. area within 50 & 200 m	$\sqrt{x}$ and ln (x+1)
Shrubs	prop. area within 50 & 200 m	$\sqrt{x}$
Subalpine conifer	prop. area within 50 & 200 m	$\sqrt{x}$ and arcsine ($\sqrt{x}$)
Wooded riparian	prop. area within 50 & 200 m	$\sqrt{x}$
Deciduous–coniferous riparian	prop. area within 50 & 200 m	$\sqrt{x}$ and arcsine ($\sqrt{x}$)
Fish and invertbrates		
Fish species presence–absence		-
Caddisfly frequency	proportion of samples	ln (x+1)
Mayfly frequency	proportion of samples	ln (x+1)
Stonefly frequency	proportion of samples	arcsine ($\sqrt{x}$)
Aquatic macroinvertebrate abundance	index derived from abund. classes	ln (x+1)
Human disturbance:		
Road density index	weighted km/ha within 200 m	ln (x+1)

Abiotic Environmental Characteristics

We described the abiotic environment at each lentic sample unit using 5 variables: elevation, orientation to Lake Tahoe, mean annual precipitation, and percent slope within 50 m and 200 m (Table 181). We obtained the elevation at the surface of the lentic sample unit from 1:24,000 USGS topographic maps. To assess orographic differences in environmental relationships, we used 4 categories of basin orientation for data analysis. We assigned each sample unit an orientation to Lake Tahoe based on geological patterns that divide regions around the basin: north side (n = 12), south side (n = 36), east side (n = 13), and west side (n = 27) (Fig. 74).

Precipitation and percent slope were derived from digital spatial data. We obtained mean annual precipitation from PRISM data (Daly et al. 1994, Daly et al. 1997, Daly and Johnson 1999). A slope polygon map was derived by interpreting topographic isoclines. The digital data for these variables represented their values as membership in value classes. Precipitation was reported in one-inch increments and was converted to centimeters. Percent slope was reported in 10 classes: 0 to 5, 6 to 15, 16 to 25, 26 to 35, 36 to 45, 46 to 55, 56 to 65, 66 to 75, 76 to 85, and 86 and greater. To derive an average value for these variables for each lentic sample unit, we performed the following steps: 1) calculated the proportion of the total area occupied by each class (for example, 10 to 19 percent slope) within 200 m (and additionally, 50 m, for slope); 2) multiplied that proportion by the average value of the class (in this example, 14.5) to obtain the contribution to the final value associated with each class; and 3) summed those values across classes to arrive at the final value for each lentic sample unit. This method yielded an average value for the area surrounding each sample unit.

Sample Unit Characteristics

Four variables described the physical characteristics of each lentic sample unit: sample unit area, perimeter, maximum depth, and substrate (Table 181). Sample unit area and perimeter were obtained from digitized USGS topographic maps or from USGS (1994) for wet meadows derived from that source. Maximum sample unit depth was determined using different techniques depending on the size of the sample unit. Values for sample units with known depths (generally the larger lakes) were obtained from Schaffer (1998) or from knowledgeable individuals. For other sample units, observers waded when possible to the deepest part of the sample unit and estimated depth to the nearest 0.1 m. For deeper sample units, observers employed a reel with a lead sinker attached to a heavy fishing line on which 1 m increments, up to 30 m, were delineated. Depth was determined by lowering the line to the bottom from an inflatable raft. Maximum lake depth was recorded as the greatest depth (to the nearest 0.5 m) obtained from 5 measurements in locations likely to be at or near the deepest part of the sample unit.

Littoral zone substrate was described during plant surveys. To obtain substrate measurements, we recorded the dominant substrate at each transect: silt, sand (particle size <2 mm), pebbles (2 to 75 mm), cobbles (5 to 300 mm), boulders (>300 mm), or bedrock. Substrate data were summarized for each sample unit as the proportion of transects dominated by each substrate type.

Vegetation Characteristics

We described the following vegetation characteristics at each sample unit: frequency of floating and submerged logs, frequency of overhanging vegetation, surrounding terrestrial vegetation, and surrounding canopy cover (Table 181).

Observers recorded 2 measures of cover at each transect during plant surveys: presence of overhanging vegetation (≤ 10 cm above the water surface) and presence of submerged or floating logs ≥ 10 cm in diameter.

Terrestrial vegetation types surrounding each sample unit were derived by a 3-step process. First, we collapsed the 12 vegetation series (excluding water, barren, and urban) identified in the basin's CalVeg vegetation layer (USDA 1991a) into 5 major vegetation types: mixed conifer, quaking aspen, subalpine conifer, shrub, and meadow (Table 182). Vegetation information for 3 sample units near the Lake Tahoe basin's eastern boundary (Luther Meadow, Mud Lake, and Star Lake) were supplemented by interpretation of aerial photographs because CalVeg information was not available beyond the Lake Tahoe basin's eastern boundary. Because riparian vegetation was generally not well represented in the CalVeg vegetation layer, we supplemented the CalVeg data with a map of riparian vegetation (USGS 1994), derived from infrared photography (see section on wet meadow selection for more details). We collapsed the 5 vegetation series identified in the basin's riparian vegetation layer (USDA 1990, USGS 1994), resulting in the identification of 3 riparian types: wooded riparian, deciduous–coniferous riparian, and meadow (Table 182). Finally, we overlaid the map of the 3 riparian vegetation types on top of the map of the 5 CalVeg vegetation types to derive a combined map, with areas of overlap being assigned the vegetation type from the riparian vegetation layer. The resulting map displayed 7 vegetation types because the "meadow" vegetation type occurred in both vegetation maps. The value for each vegetation type for each lentic unit was the proportion of the analysis area (50 m for plants, amphibians, and reptiles, and 200 m for birds) occupied by each vegetation type.

TABLE 182. Vegetation series and associated derived vegetation types for lentic sample units in the Lake Tahoe basin.

Vegetation type	Original vegetation series*
Shrub	Basin sagebrush (C)
	Huckleberry oak (C)
	Mixed alpine scrub (C)
	Montane chaparral (C)
Mixed conifer	Jeffrey pine (C)
	Mixed conifer – fir (C)
	Mixed conifer – pine (C)
Quaking aspen	Quaking aspen (C)
Subalpine conifer	Red fir (C)
	Subalpine conifer (C)
Meadow	Wet meadow (C)
	Moist meadow (R)
	Wet meadow (R)
Wooded riparian	Coniferous riparian (R)
	Deciduous riparian (R)
Deciduous–coniferous riparian	Deciduous–coniferous riparian (R)

* C = vegetation series from CalVeg vegetation layer (USDA 1991a); R = vegetation series from riparian vegetation layer (USGS 1994).

We obtained canopy cover values from the CalVeg vegetation data (USDA 1991a). Percent canopy cover was reported in 9 classes: no canopy cover, 10 to 19%, 20 to 29%, 30 to 39%, 40 to 49%, 50 to 59%, 60 to 69%, 70 to 79%, and 80 to 89%. Average canopy cover per sample unit was determined in the same manner as were average slope and precipitation (see above).

Fish and Invertebrates

We noted the presence of fish during amphibian and reptile surveys, identifying them to the lowest taxonomic level possible. Meadows were visually scanned for fish from above the water surface, as observers could readily see the bottom. If no fish were observed during bird or amphibian and reptile surveys at lakes, then we snorkeled the lake using a diving mask and inflatable raft. Lakes were snorkeled until fish were observed or for a maximum of 10 min for lakes less than 1 ac with 2 additional min per ac (for a maximum of 30 min) for larger lakes.

Aquatic macroinvertebrates were sampled with long-handled dip nets, with observers standing in place and sweeping the net in all areas of water within reach. We noted the presence of mayflies (Ephemeroptera), stoneflies (Plecoptera), and caddisflies (Tricoptera) and recorded an abundance class for all macroinvertebrates in the net (1 to 3, 4 to 10, 11 to 50, 51 to 100, 101 to 250, 250 to 500, and >500). Invertebrates were sampled 10 times at each sample unit at random points determined by timed intervals (Figs. 75 & 76). Mayfly, stonefly, and caddisfly frequencies were summarized as the proportion of samples per sample unit containing individuals from each order. We calculated an index of macroinvertebrate abundance for each sample unit by adding the minimums for each of the 10 abundance codes recorded, adding the maximums for each code, and averaging the 2 sums.

Disturbance Characteristics

We calculated a road density index around each sample unit (Table 181). Data were obtained from digitized maps of roads and trails and were checked for accuracy using aerial photos. The road density index was based on the length of trails and roads of various types per unit area weighted by a scaling factor intended to represent the relative impacts of different road and trail types. We calculated the road density index as ((8 * highway km) + (4 * other paved road km) + (2 * dirt road km) + trail km) / (total area within 200 m).

Data Analysis

All statistical tests were performed using SPSS 6.1.3 (SPSS 1990). All tests were performed at $\alpha = 0.05$, with P-values ≤ 0.10 considered ecologically significant.

Environmental Analyses

We performed Principal Components Analyses (PCAs) on 3 sets of environmental variables to describe environmental gradients: 1) macro-scale abiotic characteristics (elevation, precipitation, slope, and sample unit area); 2) substrate and aquatic vegetation characteristics (proportion bedrock, boulders, cobbles, pebbles, sand, and silt, and plant taxonomic richness and frequency); and 3) terrestrial vegetation characteristics (proportion meadow, mixed conifer, subalpine conifer, shrubs, wooded riparian, deciduous–coniferous riparian, and aspen within 200 m). After variables were transformed if necessary to better approximate a normal distribution (Table 181), macro-scale variables and sample unit characteristics were standardized into z-scores by subtracting the mean and dividing by the standard deviation. We used an Equamax rotation for all PCAs. Factors with Eigenvalues ≥ 1.0 were reported and discussed.

We compared environmental characteristics among north-, south-, east-, and west-side sample units to determine whether sample unit characteristics differed by orientation. We used one-way ANOVAs, or used Kruskal-Wallis tests when assumptions for ANOVAs were not met. We used Tukey's HSD test for unplanned multiple comparisons when ANOVA results were significant, and GT2 tests (Sokal and Rohlf 1981) when Kruskal-Wallis results were significant.

Bird Family Associations

We performed a PCA to identify patterns of association of bird families. We did not conduct the analysis at the species or genus level because of the high number of taxa and low frequency of occurrence across lentic sample units at the species and genus levels. Furthermore, the family level was appropriate for this analysis because birds in the same family often share foraging and nesting habitat associations and dietary patterns. We limited the analysis to those families occurring at 10% or more of the lentic units to ensure that the PCA reflected major gradients in family composition and abundance across sample units and was not driven by the limited distributions of a few taxa. The number of individuals in each bird family at each lentic unit was used as the dependent variable in the PCA. Average family abundance was calculated for each sample unit as the average number of birds detected in each family across all point counts. We used an Equamax rotation and included only factors with Eigenvalues ≥ 1.0.

Alpha Diversity Analyses

We used stepwise multiple linear regression to determine environmental characteristics useful for predicting bird, amphibian, and littoral zone plant alpha diversity. We used 3 sets of independent variables for deriving regression models (Table 181): 1) abiotic environmental characteristics, 2) sample unit characteristics, and 3) vegetation characteristics. We omitted sample unit perimeter from the set of sample unit characteristics because it was highly correlated with sample unit area ($r = 0.98$). To create a final model involving all types of independent variables, we took the key variables that resulted from the 3 models and entered them into a backward stepwise model, yielding a single final model (Pedlar et al. 1997, Schweiger et al. 1999).

We omitted irrelevant and redundant variables from several analyses. We regressed upland bird measures on abiotic and vegetation variables only, as sample unit variables such as substrate were not relevant to upland bird richness or abundance. When littoral zone plant measures were regressed on sample unit characteristics, they were omitted from the independent variable set. When we calculated correlations of plant species richness with environmental PCA factor scores, we included only the macro-scale and terrestrial vegetation gradients.

We performed one-way ANOVAs on the 4 basin orientations to determine whether birds, amphibians, and littoral zone plants differed in richness or abundance among sample units with in different basin orientations. We used Tukey's HSD multiple comparison procedure to determine which orientations differed from each other. When the assumptions for ANOVA were not met, we used Kruskal-Wallis tests and the GT2 procedure for multiple comparisons.

We wished to determine differential effects of elevation and disturbance on the dependent variables, but analysis of these relationships were confounded because elevation and disturbance in the basin were highly negatively correlated. To sort out the effects of disturbance for all dependent variables for which elevation was a significant predictor, we performed analyses of covariance in which elevation was grouped into classes and road density was a covariate.

Finally, we explored relationships between the alpha diversity of some groups and the occurrence of other organisms. We calculated correlations between aquatic bird alpha diversity and potential food items: plant taxonomic richness, plant frequency, caddisfly frequency, mayfly frequency, stonefly frequency, and the index of macroinvertebrate abundance. We also explored the relationship between trout presence and amphibian species richness using a t-test.

RESULTS

Environmental Characteristics

Abiotic Environmental Characteristics

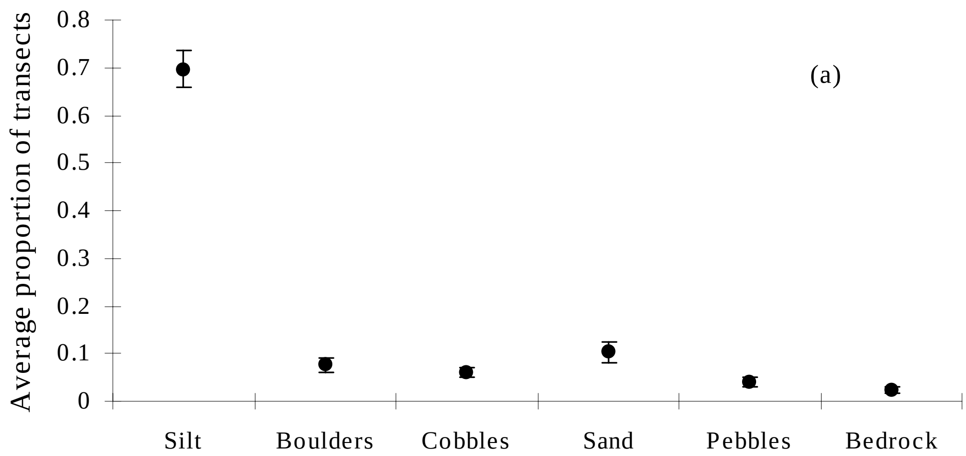
The 88 sample units varied widely in abiotic environmental conditions. Sample units ranged over 950 m in elevation, from 1898 m to near the crests of the Sierra Nevada and Carson Range, and represented a range of levels of precipitation, from relatively dry conditions at lake level (just over 50 cm/year) on the east side to much wetter conditions at high elevations on the west side (over 185 cm/year) (Table 183). The terrain surrounding sample units ranged from flat (near 0%) to steeply sloped (over 50%) (Table 183). The distribution of sample units among the 4 basin orientations was unequal, due to the availability of lentic ecosystems for sampling in the different orientations. Twenty-seven sample units were located on the west side, while 12 were on the north side, 13 were on the east side, and 36 were on the south side. Values for each sample unit are listed in Appendix 22.

Sample Unit Characteristics

A variety of substrates were observed. Silt was the most common substrate type, occurring at over 90% of sample units and dominating almost 70% of transects on average (Table 183, Fig. 77). Bedrock was the least common substrate, occurring at around 20% of sample units and dominating 2.4% of transects on average (Table 183, Fig. 77). Other substrates were intermediate in frequency and the proportion of transects they dominated (Table 183, Fig. 77). Values for each sample unit are listed in Appendix 22.

TABLE 183. Descriptive statistics of environmental features across lentic sample units (n = 88) in the Lake Tahoe basin. Frequency is the percent of sample units at which an environmental variable had a value greater than zero. Dashes indicate that the statistic was not applicable.

Environmental variable	Frequency (%)	Minimum	Maximum	Mean	SE
Abiotic environmental characteristics					
Elevation (m)	-	1898.9	2850.7	2275.8	27.17
Mean annual precipitation (cm)	-	50.6	186.2	111.9	3.50
Average % slope within 50 m	-	2.5	51.0	14.1	1.11
Average % slope within 200 m	-	2.5	45.5	17.7	1.14
Sample unit characteristics					
Area (ha)	-	0.03	570.9	13.5	6.79
Perimeter (m)	-	74.7	11752.9	1043.7	176.06
Depth (m)	-	0.1	111.2	7.1	0.016
Silt (proportion of transects)	93.2	0.0	1.00	0.70	0.039
Sand (proportion of transects)	45.5	0.0	1.00	0.10	0.023
Pebbles (proportion of transects)	33.0	0.0	0.60	0.04	0.011
Cobbles (proportion of transects)	45.5	0.0	0.62	0.06	0.012
Boulders (proportion of transects)	50.0	0.0	0.82	0.08	0.016
Bedrock (proportion of transects)	20.5	0.0	0.46	0.02	0.008
Vegetation characteristics					
Aquatic plant diversity	-	0.0	4.8	1.3	0.11
Aquatic plant frequency	-	0.0	1.00	0.74	0.034
Logs (proportion of transects)	68.2	0.0	0.74	0.17	0.020
Overhanging veg (prop. of transects)	83.0	0.0	0.78	0.23	0.021
Wooded riparian within 50 m	52.3	0.0	0.58	0.07	0.013
Wooded riparian within 200 m	76.1	0.0	0.31	0.06	0.007
Decid–con riparian within 50 m	53.4	0.0	0.58	0.09	0.014
Decid–con riparian within 200 m	71.6	0.0	0.30	0.06	0.007
Meadow within 50 m	45.5	0.0	0.84	0.10	0.021
Meadow within 200 m	58.0	0.0	0.65	0.05	0.012
Shrubs within 50 m	51.1	0.0	0.69	0.07	0.014
Shrubs within 200 m	76.1	0.0	0.63	0.14	0.016
Mixed conifer within 50 m	59.1	0.0	0.83	0.21	0.026
Mixed conifer within 200 m	62.5	0.0	0.97	0.29	0.032
Subalpine conifer within 50 m	35.2	0.0	0.82	0.09	0.018
Subalpine conifer within 200 m	42.0	0.0	0.83	0.13	0.022
Aspen within 50 m	3.4	0.0	0.08	0.002	0.001
Aspen within 200 m	5.7	0.0	0.06	0.002	0.001
Canopy cover within 50 m	-	0.0	71.3	30.4	2.14
Canopy cover within 200 m	-	0.0	69.5	26.6	1.83
Disturbance					
Rd. density index (weighted km/ha)	76.1	0.0	44.5	7.6	1.11



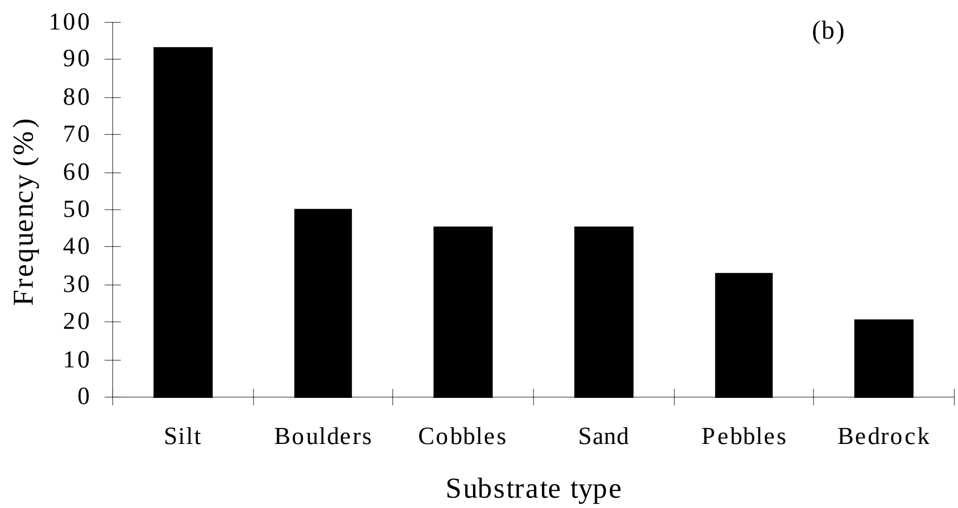


FIG. 77. Comparison of substrates along 3 m transects sampled within lentic sample units (*n* = 88) in the Lake Tahoe basin. (a) is the average proportion (± 1 SE) of transects dominated by each of 6 substrates and (b) is the frequency of each substrate.

The sizes of sample units ranged widely. Sample units ranged in area from small ponds < 1 ha to very large lakes > 570 ha. The 3 smallest sample units were Pond of the Woods, Purgatory Pond, and Limbo Pond, and the 3 largest sample units were Fallen Leaf Lake, Marlette Lake, and Upper Echo Lake. Sample unit perimeter ranged from 74.7 m to 11,752.9 m and was significantly positively correlated with sample unit area (r = 0.98, $P < 0.001$). Sample unit depth varied from 0.1 to 111.2 m and was also highly positively correlated with sample unit area (r = 0.60, $P < 0.001$). The 4 shallowest sample units were General Creek Meadow, Zephyr Meadow, North Canyon Meadow, and Upper Benwood Meadow (all 0.1 m deep), and the 3 deepest sample units were Fallen Leaf Lake, Cascade Lake, and Upper Echo Lake (all > 50 m deep). Values for each sample unit are listed in Appendix 22.

Vegetation Characteristics

Vegetation characteristics also varied widely among sample units. Logs were present at 68.2% of sample units and were present in as many as 75% of transects (Table 183). Overhanging vegetation was present at 83.0% of sample units and was present in as many as 78% of transects (Table 183). We detected 59 unique taxa of littoral zone plants overall (Appendix 24). Most of these were identified to the genus level; some could be identified as monocots or dicots only. Littoral zone plants were absent from some sample units and neared an average of 5 species per transect with 100% of transects containing plants at other sample units (Table 183).

Of the 7 vegetation classes occurring within 50 m of sample units, mixed conifer was the most common vegetation type and had the highest mean coverage (Table 183, Fig. 78). However, shrubs and wooded riparian were the most common vegetation types within 200 m of sample units, with mixed conifer having the highest mean coverage (Table 183, Fig. 79). The least common vegetation type at both scales was aspen, which also had the lowest mean coverage across sample units (Table 183, Figs. 78 & 79).

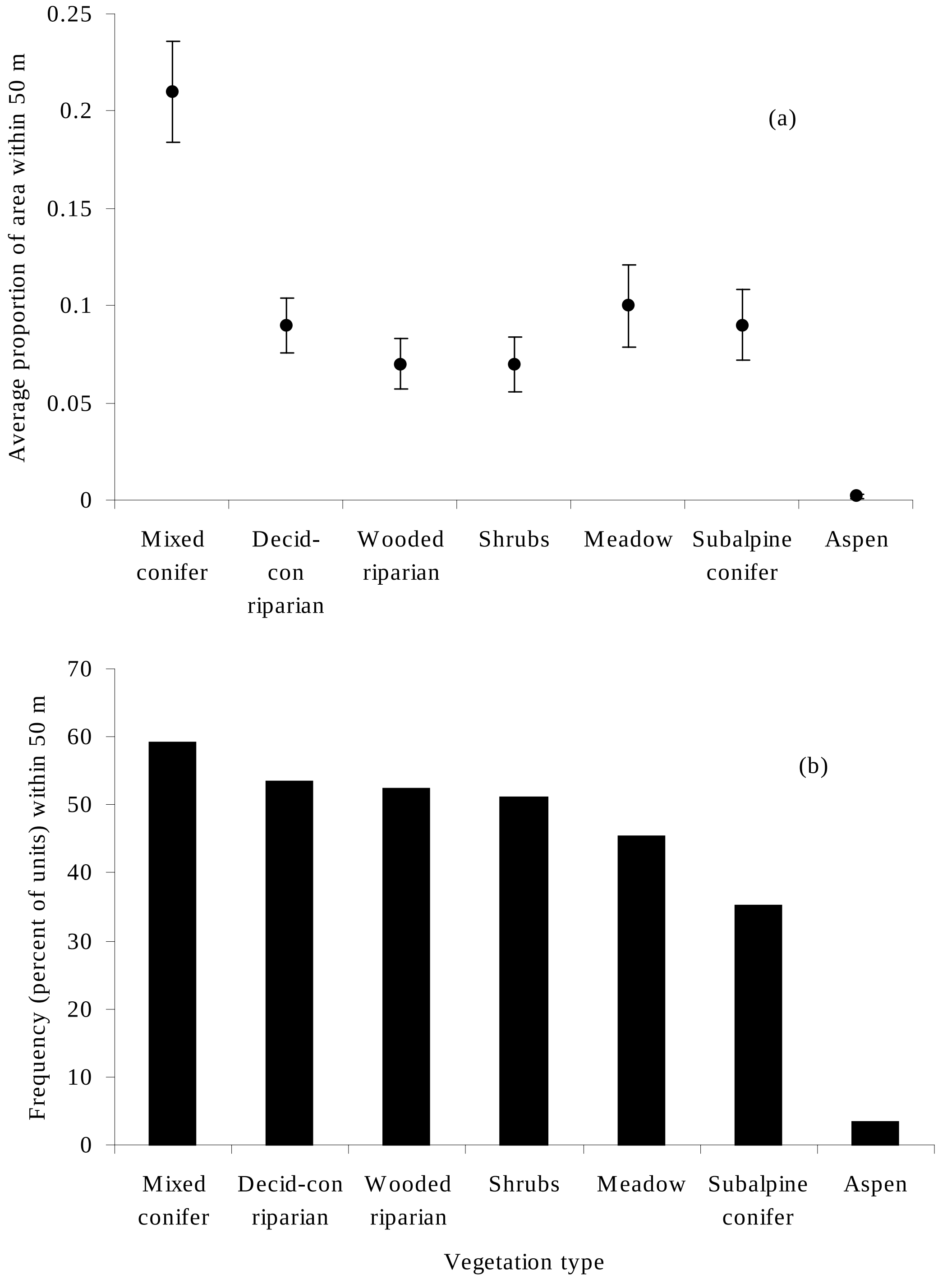


FIG. 78. Composition of vegetation types within 50 m of sample lentic sample units (n = 88) in the Lake Tahoe basin: (a) average proportion of area (± 1 SE) occupied by each vegetation type and (b) frequency of vegetation types.

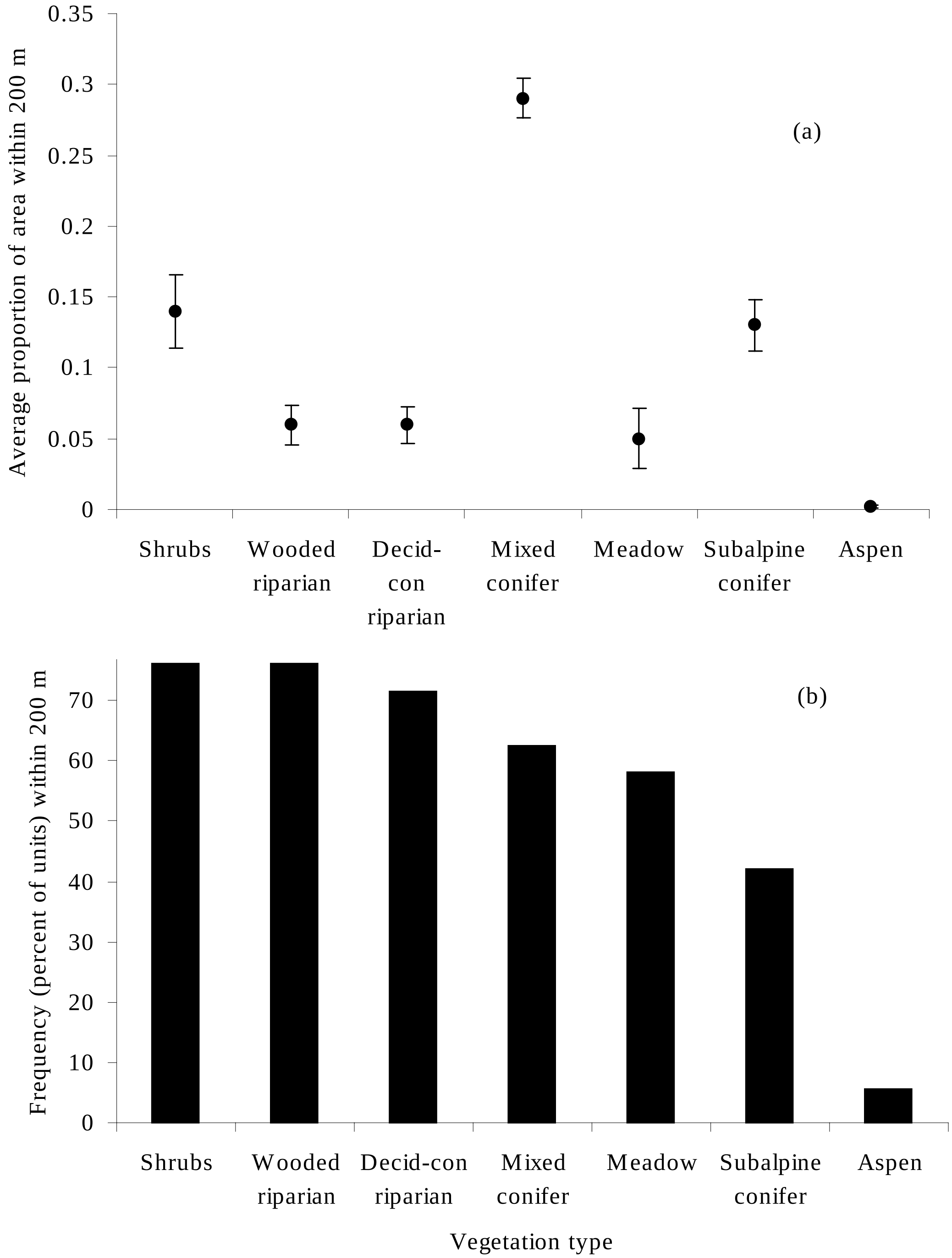


FIG. 79. Composition of vegetation types within 200 m of lentic sample units (n = 88) in the Lake Tahoe basin: (a) average proportion of area (± 1 SE) occupied by each vegetation type and (b) frequency of vegetation types.

Fish and Invertebrates

We detected fish at 43 sample units (48.9%). Overall, we detected 12 species of fish in 10 genera, 5 families, and 3 orders (Table 184). We detected salmonids at 35 sample units (39.8%), and minnows at 29 sample units (33.0%). The occurrence of salmonids and minnows overlapped significantly (χ^2_3 = 38.93, P < 0.001). Trout and minnow presence were significantly correlated with many environmental variables; both groups of fish occurred more commonly at large, deep sample units with rocky substrates (Table 185).

TABLE 184. Fish detected during amphibian and reptile surveys at lentic sample units (n = 88) in the Lake Tahoe basin. Frequency is the percent of sample units occupied.

Common name	Scientific name	Frequency (%)
Tahoe sucker	*Catostomus tahoensis*	2.3
Unidentified minnow	Cyprinidae	25.0
Koi	*Cyprinus carpio*	1.1
Mosquitofish	*Gambusia affinis*	1.1
Tui chub	*Gila bicolor*	2.3
Brown bullhead	*Ictalurus nebulosis*	5.7
Lahontan cutthroat trout	*Oncorhynchus clarkii*	1.1
Rainbow trout	*Oncorhynchus mykiss*	11.4
Kokanee salmon	*Oncorhynchus nerka*	1.1
Unidentified fish	Osteichthyes	8.0
Speckled dace	*Rhinichthys osculus*	14.8
Lahontan redside	*Richardsonius egregious*	1.1
Brown trout	*Salmo trutta*	5.7
Unidentified trout	Salmonidae	26.1
Brook trout	*Salvelinus fontinalis*	3.4

TABLE 185. Significant correlations of trout and minnow presence with environmental variables at 88 lentic sample units in the Lake Tahoe basin. P = positive correlation; n.s. = non-significant.

	Trout		Minnows	
Environmental variable	r	*P*	r	*P*
Area	0.693	<0.001	0.607	<0.001
Depth	0.664	<0.001	0.578	<0.001
Bedrock	0.347	0.001	P	n.s.
Boulders	0.417	<0.001	0.295	0.005
Cobbles	0.518	<0.001	0.379	<0.001
Pebbles	0.329	0.002	0.306	0.004
Sand	0.275	0.010	0.277	0.009
Silt	-0.454	<0.001	-0.365	<0.001
Aquatic plant diversity	-0.261	0.014	-0.192	0.073
Aquatic plant frequency	-0.352	0.001	-0.289	0.006

The presence and composition of aquatic macroinvertebrates ranged widely among sample units (Table 186). Over 95% of sample units had macroinvertebrate fauna. Of the 3 orders of macroinvertebrates recorded, caddisflies were the most commonly detected, occurring at over 75% of sample units.

TABLE 186. Focal invertebrates detected during invertebrate dip net samples at 88 lentic sample units in the Lake Tahoe basin.

Taxon	Measure	Frequency (%)	Min	Max	Mean	SE
All invertebrates	Abundance index[a]	95.5	0.0	468.5	96.5	11.53
Mayflies	Prop. of samples[b]	30.7	0.0	0.80	0.11	0.02
Stoneflies	Prop. of samples[b]	23.9	0.0	0.50	0.07	0.02
Caddisflies	Prop. of samples[b]	77.3	0.0	1.00	0.37	0.04

[a] The measure of approximate total invertebrate abundance was obtained from averaging he upper and lower bounds of abundance classes obtained from 10 samples.

[b] Numbers for mayflies, stoneflies, and caddisflies were obtained from the proportion of samples that contained individuals of those orders.

Habitat Features by Basin Orientation

Abiotic Environmental Characteristics

Mean annual precipitation was significantly greater on the west side than on all other sides of the basin, and greater on the south side than on the east side of the basin ($F_{3,84} = 21.90$, $P < 0.001$) (Fig. 80). Percent slope within 200 m was also significantly different among orientations ($F_{3,84} = 2.73$, $P = 0.049$), with west side sample units having the greatest percent slope, followed by south, east, and north side sample units (Fig. 80). However, no 2 orientations were significantly different in percent slope based on multiple comparison tests. Elevation and percent slope within 50 m were not significantly different among basin orientations.

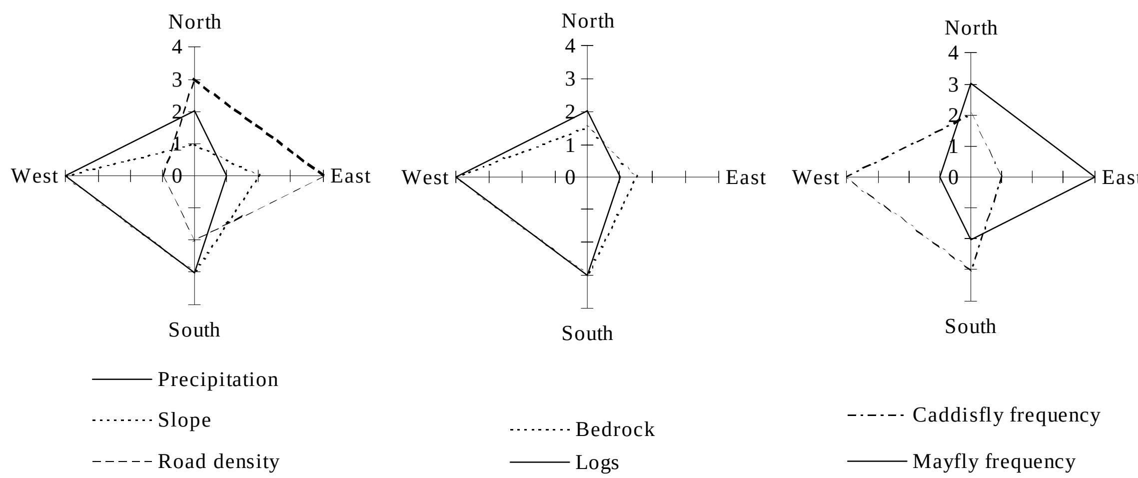


FIG. 80. Rank order of basin orientations from lowest (1) to highest (4) in precipitation, percent slope, road density, bedrock, logs, and caddisfly and mayfly frequency. Data are from 88 lentic sample units in the Lake Tahoe basin.

Sample Unit Characteristics

Proportion of bedrock was significantly different among orientations ($\chi^2_3 = 8.84$, $P = 0.032$), with west side sample units having the greatest amount of bedrock, followed by south and then east and north side sample units (Fig. 80). However, no 2 sample units were significantly different from each other in proportion of bedrock based on multiple comparison tests. Area, perimeter, depth, and all other substrate characteristics were not different among basin orientations.

Vegetation Characteristics

Frequency of floating and submerged logs was significantly greater at west and south side sample units than at east side sample units ($F_{3,84} = 4.04$, $P = 0.010$) (Fig. 80). Overhanging vegetation, plant species richness and frequency, canopy cover, and proportion of surrounding area occupied by different vegetation types were not different among basin orientations.

Invertebrates

Caddisfly frequency was significantly different among orientations ($\chi^2_3 = 20.51$, $P < 0.001$), with west side sample units having greater caddisfly frequency than east side sample units, and south side sample units having greater caddisfly frequency than east and north side sample units (Fig. 80). Mayfly frequency was also significantly different among orientations ($\chi^2_3 = 13.75$, $P = 0.003$), with east side sample units having greater mayfly frequency than west and south side sample units, and north side sample units having greater mayfly frequency than west side sample units (Fig. 80). Total aquatic invertebrate abundance and stonefly frequency were not different among basin orientations.

Environmental Gradients

Abiotic Environmental Gradients

We performed a PCA on 4 macro-scale abiotic variables. Correlations among the 4 variables were relatively low (r = -0.013 to 0.670), with 4 correlations with $P \leq 0.05$ (Table 187).

TABLE 187. Significant correlations among measures of abiotic environmental characteristics. Bolded values indicate $P \leq 0.01$. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin. Dashes indicate non-significant correlations and redundancies.

	Precipitation	Percent slope	Sample unit area
Elevation	**0.670**	**0.419**	-
Precipitation	-	**0.377**	-
Percent slope	-	-	0.250

Two factors with Eigenvalues greater than 1.0 resulted, explaining a total of 77.8% of the variation across sample units (Table 188). Factor 1 explained 50.0% of the variation and represented a gradient of increasing elevation and precipitation, with some influence of increasing percent slope. Factor 2 explained 27.8% of the variation and represented a gradient of increasing sample unit area.

TABLE 188. Abiotic macro-scale variables principal components analysis. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin.

Variable	Factor 1 score	Factor 2 score
Elevation	**0.8925**	0.0024
Precipitation	**0.8829**	-0.0378
Percent slope within 200 m	**0.6006**	0.5454
Sample unit area	-0.0889	**0.9320**
Eigenvalue	2.0	1.1
% Variation explained	50.0	27.8

Littoral Zone Plant and Substrate Gradients

We performed a PCA on 8 substrate and littoral zone plant variables. Correlations among the 8 variables were low to high (r = 0.047 to 0.891), with 24 correlations with $P \leq 0.05$ (Table 189).

TABLE 189. Significant correlations among measures of littoral zone plant and substrate characteristics. Bolded values indicate $P \leq 0.01$. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin. Dashes indicate non-significant correlations and redundancies.

	Sand	Pebbles	Cobbles	Boulders	Bedrock	Plant sp. rich.	Plant freq.
Silt	**-0.768**	**-0.382**	**-0.675**	**-0.714**	**-0.324**	**0.714**	**0.805**
Sand	-	-	**0.292**	0.265	-	**-0.433**	**-0.513**
Pebbles	-	-	**0.494**	-	-	-0.227	-0.261
Cobbles	-	-	-	**0.575**	**0.310**	**-0.489**	**-0.563**
Boulders	-	-	-	-	**0.407**	**-0.623**	**-0.689**
Bedrock	-	-	-	-	-	**-0.327**	**-0.347**
Plant sp. rich.	-	-	-	-	-	-	**0.891**

Three factors with Eigenvalues greater than 1.0 resulted, explaining a total of 81.0% of the variation across sample units (Table 190). Factor 1 explained 54.6% of the variation and represented a gradient of substrate productivity: increasing silt and littoral zone plant diversity and frequency and decreasing sand. Factor 2 explained 13.7% of the variation and represented bedrock and boulders, with a lack of littoral zone plants. Factor 3 explained 12.7% of the variation and represented small-diameter rock substrates.

TABLE 190. Principal components analysis of substrate and aquatic vegetation composition at 88 lentic sample units in the Lake Tahoe basin.

Variable	Factor 1 score	Factor 2 score	Factor 3 score
Silt	**0.8084**	-0.3617	-0.3899
Sand	**-0.8995**	-0.1181	0.0943
Aquatic plant frequency	**0.7198**	-0.5282	-0.2385
Aquatic plant diversity	**0.6669**	-0.5247	-0.1852
Bedrock	0.0560	**0.8449**	0.0391
Boulders	-0.4428	**0.7027**	0.1976
Cobbles	-0.3009	0.4318	**0.6942**
Pebbles	-0.0539	-0.0585	**0.9447**
Eigenvalue	4.4	1.1	1.0
% Variation explained	54.6	13.7	12.7

Vegetation Community Gradients

We conducted a PCA on the proportion within 200 m of 7 terrestrial vegetation types to elucidate the major gradients of variation in vegetation community type. Correlations among the 7 variables were relatively low (r = 0.005 to –0.600), with 3 correlations with $P \leq 0.05$ (Table 191).

TABLE 191. Significant correlations among measures of terrestrial vegetation characteristics. Bolded values indicate $P \leq 0.01$. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin.

	Subalpine conifer	Shrubs	Meadow
Mixed conifer	**-0.600**	-0.220	-0.216

Three factors with Eigenvalues greater than 1.0 resulted, explaining a total of 59.5% of the variation among sample units (Table 192). Factor 1 explained 25.7% of the total variation and represented an elevation gradient, as described by a positive association with subalpine conifer and shrubs and a negative association with mixed conifer. Factor 2 explained 17.3% of the total variation and represented the dominance of aspen versus meadow at sample units. Factor 3 explained 16.5% of the variation and represented riparian vegetation.

TABLE 192. Principal components analysis of vegetation community composition at 88 lentic sample units in the Lake Tahoe basin.

Variable	Factor 1 score	Factor 2 score	Factor 3 score
Mixed conifer	**-0.8463**	0.1537	0.0950
Subalpine conifer	**0.8472**	-0.0526	0.1502
Shrubs	**0.4260**	0.3204	-0.2785
Aspen	0.0951	**0.7851**	0.2002
Meadow	0.2267	**-0.5906**	0.1735
Wooded riparian	-0.1569	0.2750	**0.7251**
Deciduous–coniferous riparian	0.1200	-0.2025	**0.7099**
Eigenvalue	1.8	1.2	1.2
% Variation explained	25.7	17.3	16.5

Correlations Among Environmental Gradients

Several environmental gradients were significantly correlated with one another. The elevation–precipitation gradient was significantly positively correlated with the mixed to subalpine conifer gradient and the bedrock–boulders gradient; the sample unit area gradient was significantly positively correlated with the aspen to meadow gradient, the bedrock–boulders gradient, and the cobbles–pebbles gradient; the aspen to meadow gradient was significantly negatively correlated with the sand to silt gradient; and the riparian vegetation gradient was significantly negatively correlated with the cobbles–pebbles gradient (Table 193).

TABLE 193. Significant ($P \leq 0.10$) correlations among environmental gradients. Bolded values indicate $P \leq 0.05$. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin. Dashes indicate non-significant correlations and redundancies.

	Elevation–precipitation	Sample unit area	Sand to silt	Bedrock–boulders	Cobbles–pebbles
Elevation–precipitation	-	-	-	0.427	-
Sample unit area	-	-	-	0.285	0.320
Subalpine vegetation	0.558	-	-	-	-
Aspen to meadow	-	0.247	-0.244	-	-
Riparian vegetation	-	-	0.185	-	-0.196

Human Disturbance

The 88 sample units varied widely in the amount of disturbance within 200 m (Table 183, Appendix 22), although most sample units had low disturbance (Fig. 81). Roads and trails within 200 m occurred at 67 sample units (76.1%). Wildwood Basin had the highest road density index (44.5), followed by Tallac Lagoon (38.7) and Birdie Pond (36.4).

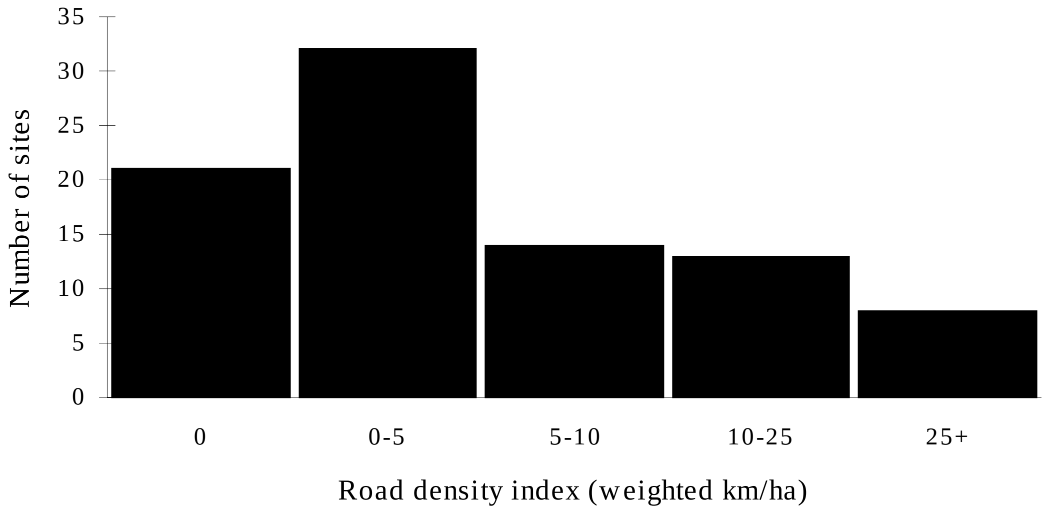


FIG. 81. Distribution of sample units across intervals of road density index values (weighted km/ha) within 200 m of 88 lentic sample units in the Lake Tahoe basin. Road density index = ((8 * highway km) + (4 * other paved road km) + (2 * dirt road km) + trail km) / (total area within 200 m).

Measured disturbance in terms of road density index corresponded well with Recreation Opportunity Spectrum classes (USDA 1988), indicating that the classes, which were used to post-stratify lakes by disturbance for sampling, were a good approximation of actual disturbance. The road density index was significantly different among ROS classes ($\chi^2_{KW} = 33.04$, $P < 0.001$); lakes in the high class had a higher road density index than lakes in the moderate and low classes, and lakes in the moderate class had significantly higher road density index than lakes in the low class in multiple comparison tests (Table 194).

TABLE 194. Average values for road density index in classes derived from 3 Recreation Opportunity Spectrum categories. Data are from 88 lentic sample units in the Lake Tahoe basin.

ROS class[a]	Average road density index[b]
Low (n = 30)	0.71
Moderate (n = 24)	1.74
High (n = 18)	2.61

[a] From USDA (1988).

[b] Road density index = ((8 * highway km) + (4 * other paved road km) + (2 * dirt road km) + trail km) / (total area within 200 m).

Disturbance and Environmental Characteristics

We explored correlations among 25 environmental variables and the road density index. Fifteen of these correlations were significant (Table 195), and the negative relationships with elevation and precipitation were particularly strong (Fig. 82).

TABLE 195. Significant correlations of the road density index with 15 environmental variables. Data are from 88 lentic sample units in the Lake Tahoe basin.

Environmental variable	r	*P*
Meadow (50 m)	0.388	<0.001
Meadow (200 m)	0.261	0.014
Mixed conifer (50 m)	0.198	0.065
Mayfly frequency	0.368	<0.001
Elevation	-0.511	<0.001
Precipitation	-0.640	<0.001
Percent slope (50 m)	-0.223	0.037
Percent slope (200 m)	-0.445	<0.001
Bedrock	-0.222	0.038
Boulders	-0.221	0.038
Deciduous–coniferous riparian (50 m)	-0.246	0.021
Subalpine conifer (50 m)	-0.253	0.017
Subalpine conifer (200 m)	-0.248	0.020
Logs	-0.429	<0.001
Caddisfly frequency	-0.361	0.001

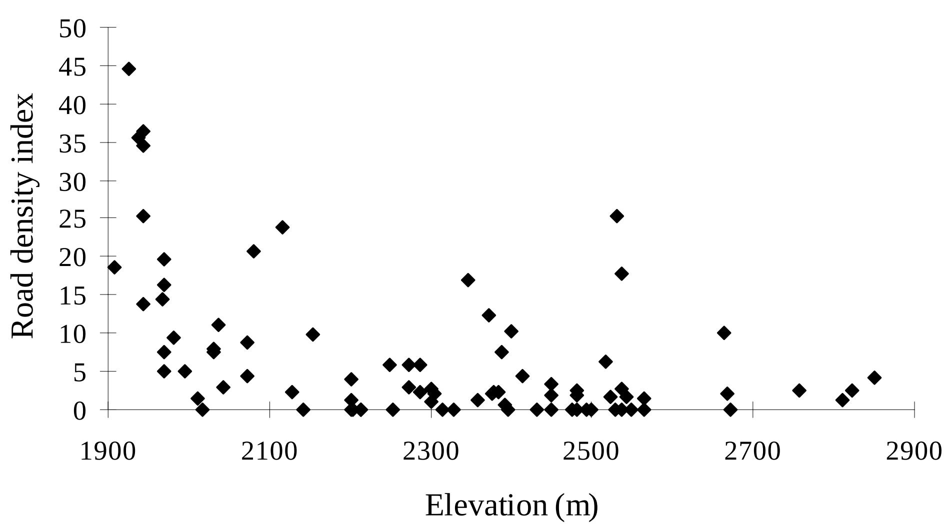


FIG. 82. Relationship of road density index to elevation at 88 lentic sample units in the Lake Tahoe basin. Road density index = ((8 * highway km) + (4 * other paved road km) + (2 * dirt road km) + trail km) / (total area within 200 m).

Disturbance by Basin Orientation

Road density was significantly different among orientations ($\chi^2_3 = 27.99$, $P < 0.001$); east side sample units had significantly greater road density than west and south side sample units, and north side sample units had significantly greater road density than west side sample units in multiple comparison tests (Fig. 80, Fig. 83).

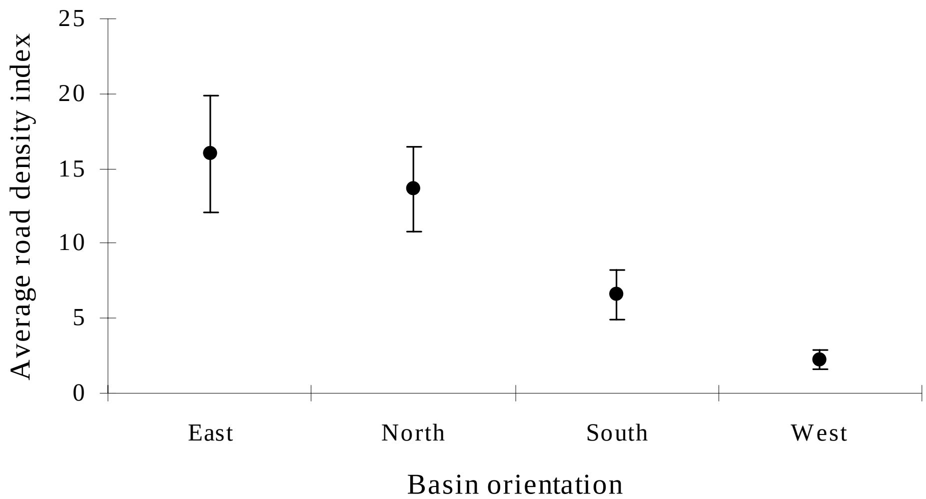


FIG. 83. Average road density index (±1 SE) for each of 4 basin orientations. Data are from 88 lentic sample units in the Lake Tahoe basin. Road density index = ((8 * highway km) + (4 * other paved road km) + (2 * dirt road km) + trail km) / (total area within 200 m).

Patterns of Bird Diversity

Patterns of Bird Alpha Diversity

General Patterns

A total of 92 native bird species were detected in point counts (Appendix 25). Bird species richness per point count ranged from 3.5 to 19.8 ($\bar{x}$ = 10.95, SE = 0.39; Appendix 23). Site bird diversity, the total number of species per sample unit, ranged from 4 to 41 ($\bar{x}$ = 14.73, SE = 0.74; Appendix 23). Bird abundance per point count ranged from 6.0 to 71.3 individuals ($\bar{x}$ = 23.46, SE = 1.29; Appendix 23). Total bird abundance ranged from 6 to 327 individuals ($\bar{x}$ = 45.18, SE = 5.06); Appendix 23). The sample units with the highest values for these 3 measures are listed in Table 196. Average bird species richness was highly positively correlated with average bird abundance (r = 0.693, $P < 0.001$) (Fig. 84). Site bird diversity was highly positively correlated with total abundance (r = 0.847, $P < 0.001$) (Fig. 85). Total abundance was not analyzed further.

TABLE 196. Sample units with the greatest bird species richness (average number of species detected per point count), site bird diversity (total number of species at a sample unit), bird abundance (average number of individual birds detected per point count), and total abundance (total number of individual birds at a sample unit), out of 88 lentic sample units in the Lake Tahoe basin.

Bird species richness		Site bird diversity		Bird abundance		Total abundance	
#	Sample unit	#	Sample unit	#	Sample unit	#	Sample unit
19.8	Tallac Lagoon	41	Fallen Leaf Lake	71.3	Spooner Lake	327	Fallen Leaf Lake
19.0	Grass Lake-LP	37	Marlette Lake	58.3	Tallac Lagoon	232	Tallac Lagoon
18.7	Luther Meadow	34	Tallac Lagoon	52.0	Folsom Spr. Pond	194	Marlette Lake

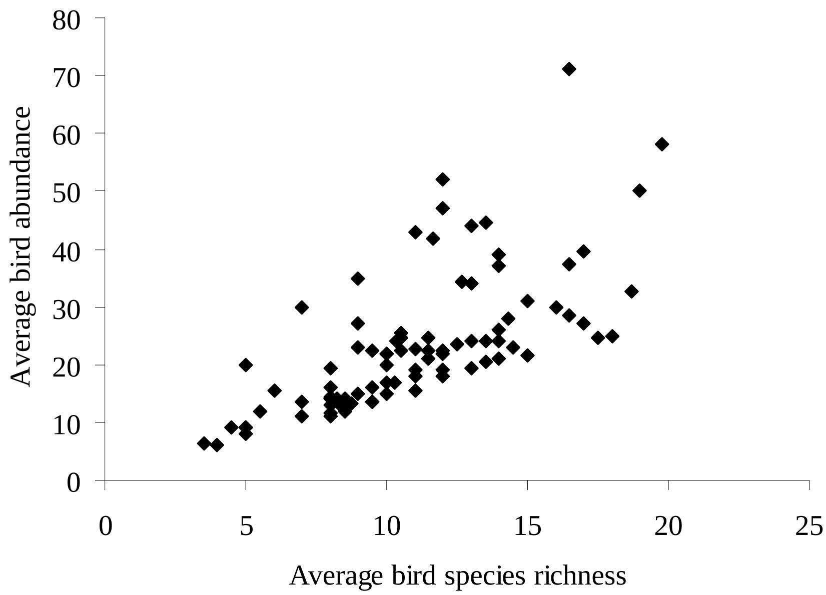


FIG. 84. Relationship between bird abundance and bird species richness at 88 lentic sample units in the Lake Tahoe basin.

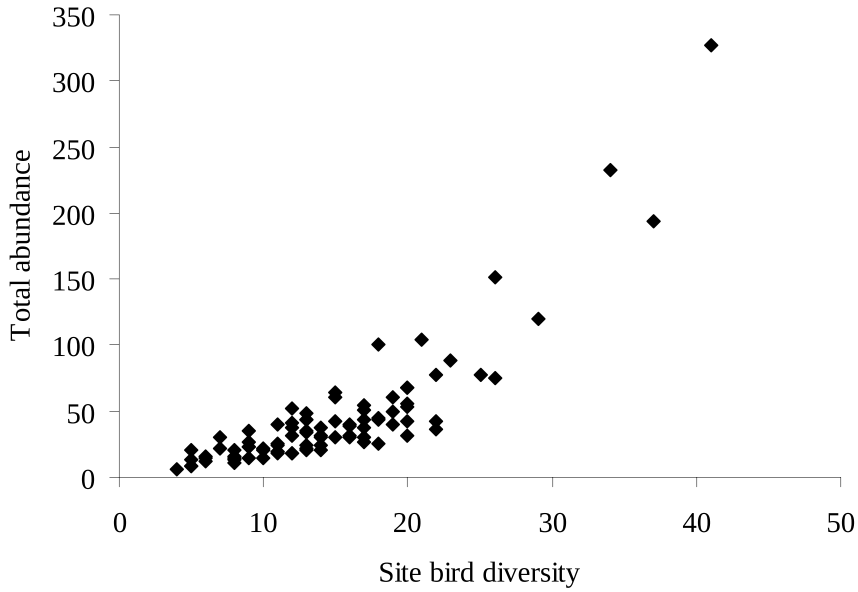


FIG. 85. Relationship between site bird diversity and total abundance at 88 lentic sample units in the Lake Tahoe basin.

Environmental Relationships of Bird Species Richness

Regression Model for Bird Species Richness. Bird species richness was significantly correlated ($P \leq 0.10$) with 8 environmental variables (Table 197). Regression of bird species richness on abiotic environmental variables resulted in a 2-variable model: negative associations with elevation and slope (adj. $R^2 = 0.310$; Table 198). Regression of bird species richness on sample unit variables resulted in a 3-variable model: a positive association with area and negative associations with bedrock and boulders (adj. $R^2 = 0.162$; Table 198). Regression of bird species richness on vegetation variables resulted in a 4-variable model: positive associations with wooded riparian, meadow, mixed conifer, and plant frequency (adj. $R^2 = 0.399$; Table 198). Backward stepwise regression on the 9 key variables resulted in a final 3-variable model: positive associations with wooded riparian and meadow and a negative association with elevation ($F_{3,84} = 24.42$, $P < 0.001$, adj. $R^2 = 0.447$; Tables 198 & 199).

TABLE 197. Significant correlations of bird species richness with 8 environmental variables at 88 lentic sample units in the Lake Tahoe basin.

Environmental variable	r	*P*
Canopy cover	0.361	0.001
Wooded riparian	0.418	<0.001
Meadow	0.197	0.066
Mixed conifer	0.424	<0.001
Elevation	-0.536	<0.001
Precipitation	-0.327	0.002
Percent slope	-0.400	<0.001
Subalpine conifer	-0.273	0.010

TABLE 198. Variables selected in stepwise regressions of 3 groups of environmental variables and bird species richness. N = negative association and P = positive association at $P \leq 0.10$. Bolded = selected in the final regression at $P \leq 0.05$ on key variables from each group of environmental variables. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin.

Environmental variable	Bird species richness
Abiotic environment:	
Elevation	**N**
Slope	N
Sample unit characteristics:	
Area	P
Bedrock	N
Boulders	N
Vegetation characteristics:	
Wooded riparian	**P**
Meadow	**P**
Mixed conifer	P
Aquatic plant frequency	P
Variables in final model	*3*
adj. R^2	*0.447*

TABLE 199. Final regression model of key environmental variables related to bird species richness at lentic sample units (n = 88) in the Lake Tahoe basin. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	P
Elevation	-0.725	0.112	-0.523	-6.458	< 0.001
Wooded riparian	7.266	2.102	0.279	3.457	0.001
Meadow	6.448	1.677	0.308	3.844	< 0.001

The observed negative relationship between bird species richness and elevation could be influenced by disturbance at lower elevations. An analysis of covariance with elevation partitioned into 4 groups and road density index as a covariate showed that elevation was significantly associated with bird species richness even after the influence of disturbance was removed (Table 200).

TABLE 200. Analysis of covariance exploring the relationship between bird species richness and elevation with disturbance (road density) as a covariate. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin. SS = sum of squares; ν = degrees of freedom; MS = mean square.

Source of variation	SS	ν	MS	F	P
Within + residual	768.43	83	9.26		
Regression	91.25	1	91.25	9.86	0.002
Elevation	273.95	3	91.32	9.86	< 0.001
Model	423.89	4	105.97	11.45	< 0.001
Total	1192.32	87	13.70		

We examined scatter plots of bird species richness against the 3 environmental variables in the final regression model to elucidate potential environmental thresholds. No thresholds were evident.

Bird Species Richness by Basin Orientation. Bird species richness did not vary by basin orientation (N = 10.7, S = 11.4, E = 12.3, W = 9.9, $F_{3,84} = 1.46$, $P = 0.231$).

Regression Model for Site Bird Diversity. Regression of site bird diversity on sample unit variables resulted in a 2-variable model: a positive association with area and a negative association with bedrock ($F_{2,85} = 31.32$, $P < 0.001$, adj. $R^2 = 0.411$; Table 201).

TABLE 201. Regression model of key environmental variables related to site bird diversity at sample lentic sample units (*n* = 88) in the Lake Tahoe basin. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	*P*
Area	2.376	0.301	0.672	7.888	< 0.001
Bedrock	-10.439	3.953	-0.225	-2.641	0.010

Correlations with Environmental Gradients. Bird species richness and site bird diversity were each significantly correlated with several environmental gradients (Table 202). Both were negatively correlated with the elevation–precipitation gradient and the associated subalpine vegetation gradient. Site bird diversity was positively correlated with area, whereas the average richness per point count was positively correlated with riparian vegetation and negatively correlated with rocky, less productive substrates.

TABLE 202. Significant correlations of bird species richness and site bird diversity with environmental gradients at 88 lentic sample units in the Lake Tahoe basin.

Environmental gradient	r	*P*
Bird species richness:		
Riparian vegetation	0.281	0.008
Bedrock–boulders	-0.367	<0.001
Elevation–precipitation–slope	-0.525	<0.001
Subalpine vegetation	-0.380	<0.001
Site bird diversity		
Area	0.534	<0.001
Elevation–precipitation–slope	-0.455	<0.001
Subalpine vegetation	-0.247	0.020

Environmental Relationships of Bird Abundance

Regression Model for Bird Abundance. Bird abundance was significantly correlated ($P \leq 0.10$) with several environmental variables (Table 203). Regression of abiotic environmental variables on bird abundance resulted in a 2-variable model: negative associations with precipitation and slope (adj. $R^2 = 0.339$; Table 204). Regression of sample unit variables on bird abundance resulted in a 3-variable model: a positive association with area and negative associations with bedrock and boulders (adj. $R^2 = 0.174$; Table 204). Regression of vegetation variables on bird abundance resulted in a 3-variable model: positive associations with meadow and mixed conifer and a negative association with canopy cover (adj. $R^2 = 0.289$; Table 204). Backward stepwise regression on the 8 key variables resulted in a 4-variable model: positive associations with area and meadow and negative associations with precipitation and slope ($F_{3,84}$ = 21.80, $P < 0.001$, adj. $R^2 = 0.489$; Tables 204 & 205).

TABLE 203. Significant correlations of bird abundance with environmental variables at 88 lentic sample units in the Lake Tahoe basin.

Environmental variable	r	*P*
Meadow	0.378	<0.001
Mixed conifer	0.238	0.026
Elevation	-0.486	<0.001
Precipitation	-0.506	<0.001
Percent slope	-0.481	<0.001
Shrubs	-0.182	0.091
Subalpine conifer	-0.231	0.030

TABLE 204. Variables selected in stepwise regressions of 3 groups of environmental variables and bird abundance. N = negative association and P = positive association at $P \leq 0.10$. Bolded = selected in the final regression at $P \leq 0.05$ on key variables from each group of environmental variables. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin.

Environmental variable	Bird abundance
Abiotic environment:	
Precipitation	**N**
Slope	**N**
Sample unit characteristics:	
Area	**P**
Bedrock	N
Boulders	N
Vegetation characteristics:	
Meadow	**P**
Mixed conifer	P
Canopy cover	N
Variables in final model	*4*
adj. R^2	*0.489*

TABLE 205. Final regression model of key environmental variables related to bird abundance at lentic sample units (n = 88) in the Lake Tahoe basin. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	*P*
Precipitation	-0.146	0.031	-0.396	-4.680	< 0.001
Slope	-0.338	0.104	-0.298	-3.267	0.002
Meadow	22.257	5.573	0.325	3.994	< 0.001
Area	1.353	0.501	0.218	2.701	0.008

The observed relationship between bird abundance and precipitation could be a consequence of human disturbance being higher at sites with lower precipitation. An analysis of covariance with precipitation partitioned into 4 groups and road density index as a covariate showed that precipitation was significantly associated with bird abundance even after the influence of disturbance was removed (Table 206).

TABLE 206. Analysis of covariance exploring the relationship between bird abundance and precipitation with road density index as a covariate. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin. SS = sum of squares; ν = degrees of freedom; MS = mean square.

Source of variation	SS	ν	MS	F	*P*
Within + residual	7956.53	83	95.86		
Regression	500.79	1	500.79	5.22	0.025
Precipitation	1166.02	3	388.67	4.05	0.010
Model	4840.39	4	1210.10	12.62	< 0.001
Total	12796.92	87	147.09		

We examined scatter plots of bird abundance against the 4 environmental variables in the final regression model to elucidate potential environmental thresholds. No thresholds were evident.

Bird Abundance by Basin Orientation. Bird abundance was significantly different among the 4 basin orientations (N = 25.0, S = 23.1, E = 35.0, W = 17.8, χ^2_{KW} = 13.43, P = 0.004), with bird abundance on the east side being significantly greater than on the west and south sides of the basin based on multiple comparison tests.

Correlations with Environmental Gradients. Bird abundance was significantly correlated with several environmental gradients (Table 207). As observed for bird species richness, abundance was negatively correlated with the elevation–precipitation gradient, subalpine vegetation, and rocky substrates. Uniquely, bird abundance was greater in association with meadows as opposed to aspen-dominated areas.

TABLE 207. Significant correlations of bird abundance with environmental gradients at 88 lentic sample units in the Lake Tahoe basin.

Environmental gradient	r	*P*
Bedrock–boulders	-0.366	<0.001
Elevation–precipitation–slope	-0.460	<0.001
Subalpine vegetation	-0.275	0.009
Aspen to meadow	-0.208	0.052

Patterns of Bird Alpha Diversity by Habitat Association

General Patterns

Patterns of bird species richness and abundance were explored in relation to associations with 3 major habitat conditions: aquatic, riparian–meadow, and upland. Site bird diversity by habitat association was not analyzed beyond these descriptive statistics. Every sample unit had at least 3 upland bird species, whereas aquatic and riparian–meadow birds were entirely absent at some sample units (Table 208, Appendix 23). The sample units with the highest values for each measure are listed in Table 209. For each habitat grouping, some species were especially abundant (Figs. 86, 87, & 88) while others occurred at very few sample units. Mallard was by far the most frequently occurring aquatic bird species, whereas 3 riparian–meadow species were tied for the most frequently occurring: Brewer's Blackbird, Brown-headed Cowbird, and Song Sparrow. Among upland species, Mountain Chickadee occurred at nearly every sample unit. Many upland species had a higher frequency of occurrence than any aquatic or riparian–meadow species, with 7 species occurring at > 50% of the sample units.

TABLE 208. Descriptive statistics for the bird species richness and abundance of 3 habitat groups. Species richness is the average number of species per point count. Site bird diversity is the total number of bird species per sample unit. Abundance is the average abundance of individual birds per point count. Total abundance is the total number of individual birds per sample unit. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin.

Habitat group	Total species	Freq (%)	Measure	Min	Max	Avg	SE
Aquatic	20	51.1	Species richness	0.0	8.0	0.83	0.14
			Site bird diversity	0.0	8.0	1.17	0.19
			Abundance	0.0	41.8	2.76	0.66
			Total abundance	0.0	68.0	5.09	1.30
Riparian–meadow	21	76.1	Species richness	0.0	7.0	1.81	0.19
			Site bird diversity	0.0	9.0	2.53	0.26
			Abundance	0.0	43.0	5.07	0.86
			Total abundance	0.0	88.0	9.20	1.57
Upland	51	100.0	Species richness	3.0	16.0	8.32	0.30
			Site bird diversity	3.0	28.0	11.02	0.50
			Abundance	5.0	30.0	15.64	0.60
			Total abundance	5.0	236.0	30.89	3.25

TABLE 209. Maximum values for bird species richness, site bird diversity, and bird abundance at 88 lentic sample units in the Lake Tahoe basin.

	Bird species richness		Site bird diversity		Bird abundance	
	#	Sample unit(s)	#	Sample unit(s)	#	Sample unit(s)
Aquatic	8.0	Grass Lake-LP[a]	8	Grass Lake-LP[a]	41.8	Spooner Lake
	4.0	Tallac Lagoon	6	Tallac Lagoon	21.0	Grass Lake-LP[a]
	4.0	Spooner Lake	6	Fallen Leaf Lake	21.0	Meiss Lake
	4.0	Lily Lake				
	4.0	Birdie Pond				
Riparian–meadow	7.0	Birdie Pond	9	Tallac Lagoon	43.0	Folsom Spr. Pond
	7.0	Folsom Spr. Pond	9	Fallen Leaf Lake	32.5	Horsehead Mdw.
	6.0	Horsehead Mdw.	8	Grass Lake-GA[b]	25.3	Edgewood Lake
			8	Spooner Lake		
Upland	16.0	Dollar Reservoir	28	Marlette Lake	30.0	Mud Lake
	15.0	Overlook Mdw.	26	Fallen Leaf Lake	28.5	Snow Creek Mdw.
	14.3	Luther Meadow	20	Luther Meadow	28.0	Seneca Pond

[a] Grass Lake at Luther Pass
[b] Grass Lake at Glen Alpine

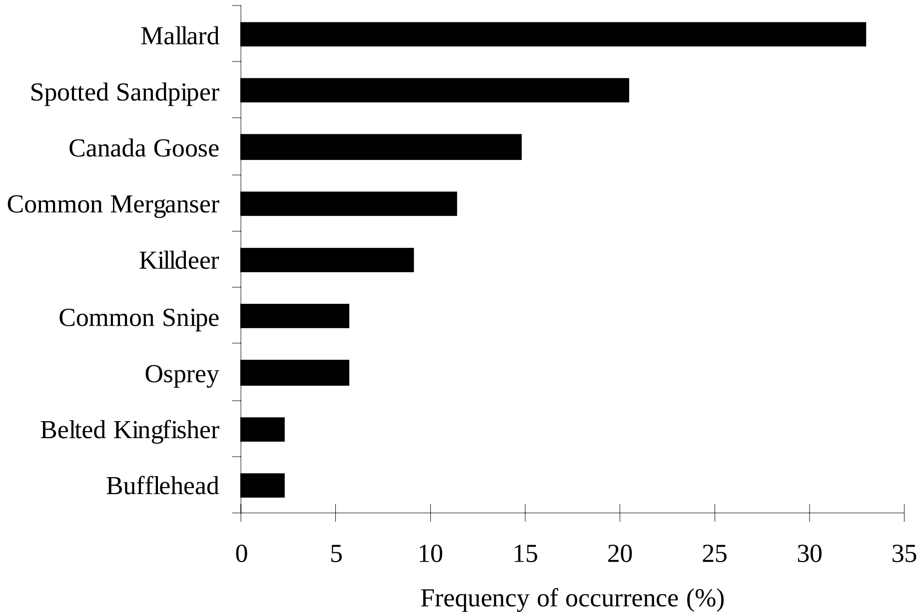


FIG. 86. The most frequently-occurring aquatic bird species at 88 lentic sample units in the Lake Tahoe basin.

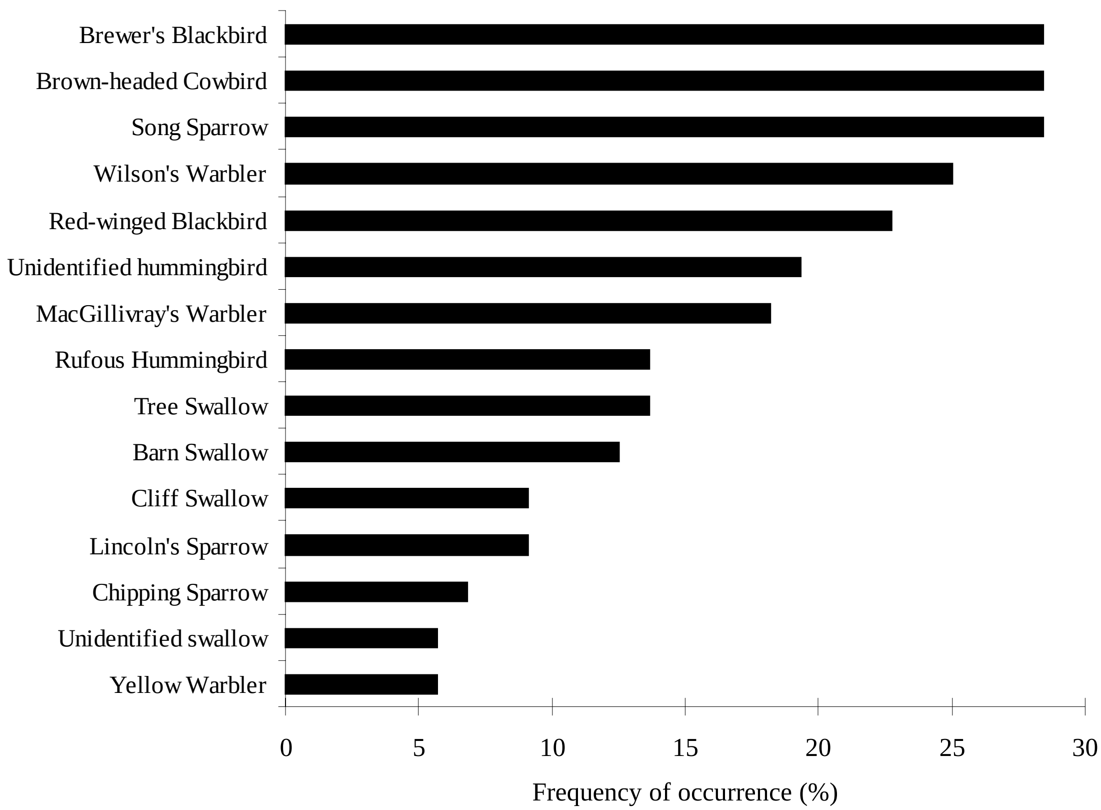


FIG. 87. The most frequently-occurring riparian–meadow bird species at 88 lentic sample units in the Lake Tahoe basin.

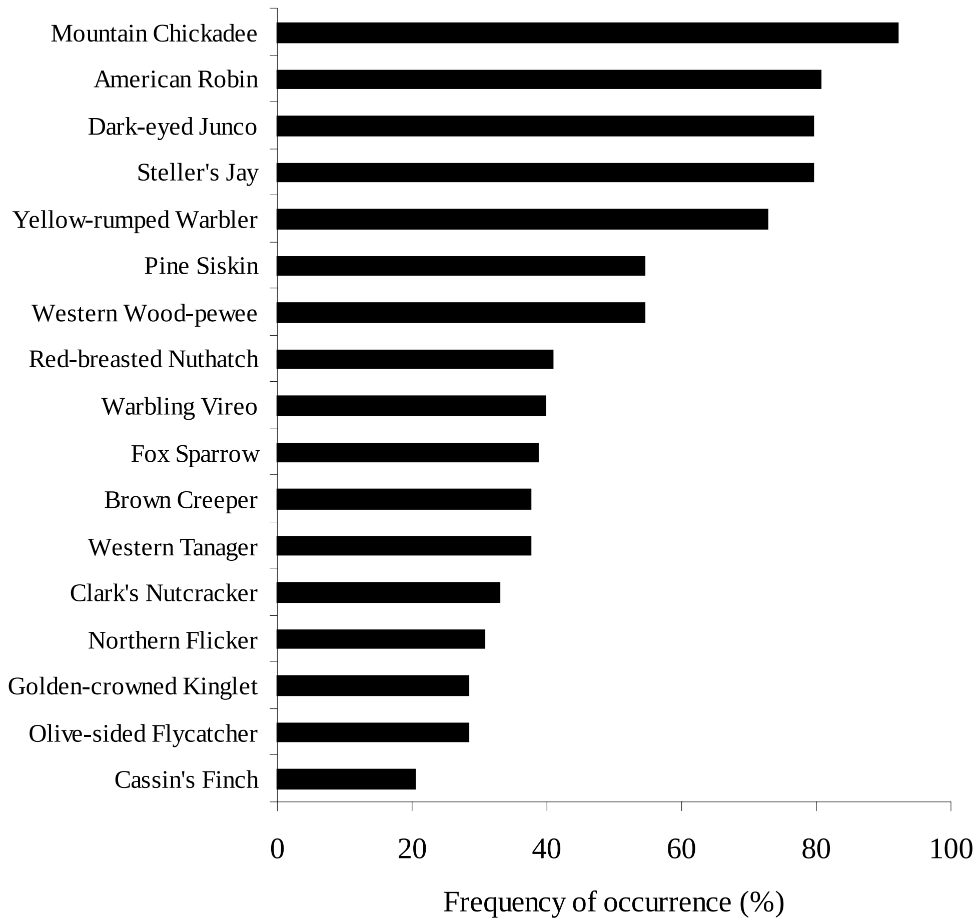


FIG. 88. The most frequently-occurring upland bird species detected at 88 lentic sample units in the Lake Tahoe basin.

Environmental Relationships of Habitat Groups

Regression Model for Aquatic Bird Species Richness. Aquatic bird species richness was significantly correlated with several environmental variables (Table 210). Regression of aquatic bird species richness on abiotic environmental variables resulted in a 2-variable model: negative associations with elevation and slope (adj. $R^2 = 0.151$; Table 211). Regression of aquatic bird species richness on sample unit variables resulted in a 2-variable model: a positive association with area and a negative association with boulders (adj. $R^2 = 0.109$; Table 211). Regression of aquatic bird species richness on vegetation variables resulted in a 3-variable model: a positive association with meadow and negative associations with logs and subalpine conifer (adj. $R^2 = 0.268$; Table 211). Backward stepwise regression on these 7 key variables resulted in a final 3-variable model: positive associations with area and meadow and a negative association with elevation ($F_{3,84} = 19.90$, $P < 0.001$, adj. $R^2 = 0.395$; Tables 211 & 212).

TABLE 210. Correlations between bird species richness for 3 habitat groups and 25 environmental variables. Bolded values indicate $P \leq 0.05$. N and P indicate non-significant (n.s.) negative and positive correlations, respectively. We did not calculate correlations between sample unit characteristics, some vegetation characteristics, and upland bird species richness; thus, “n/a” is reported for these pairings.

	Habitat group					
	Aquatic		Riparian–meadow		Upland	
Environmental variable	r	*P*	r	*P*	r	*P*
Abiotic environment:						
Elevation	-0.373	<0.001	-0.586	<0.001	N	n.s.
Precipitation	-0.356	0.001	-0.498	<0.001	P	n.s.
Slope	-0.317	0.003	-0.537	<0.001	N	n.s.
Sample unit characteristics:						
Area	0.263	0.013	P	n.s.	n/a	n/a
Perimeter	0.317	0.003	P	n.s.	n/a	n/a
Depth	P	n.s.	N	0.044	n/a	n/a
Bedrock	N	n.s.	-0.203	0.058	n/a	n/a
Boulders	N	n.s.	-0.324	0.002	n/a	n/a
Cobbles	N	n.s.	N	n.s.	n/a	n/a
Pebbles	P	n.s.	P	n.s.	n/a	n/a
Sand	P	n.s.	N	n.s.	n/a	n/a
Silt	N	n.s.	0.241	0.024	n/a	n/a
Vegetation characteristics:						
Logs	-0.329	0.002	-0.388	<0.001	n/a	n/a
Overhanging vegetation	N	n.s.	N	n.s.	n/a	n/a
Aquatic plant diversity	0.186	0.083	0.495	<0.001	n/a	n/a
Aquatic plant frequency	P	n.s.	0.416	0.001	n/a	n/a
Canopy cover	N	n.s.	P	n.s.	0.513	<0.001
Wooded riparian	P	n.s.	0.262	0.014	0.313	0.003
Deciduous–coniferous riparian	N	n.s.	N	n.s.	0.222	0.038
Meadow	0.435	<0.001	0.328	0.002	N	n.s.
Shrubs	N	n.s.	-0.213	0.047	P	n.s.
Mixed conifer	P	n.s.	0.232	0.029	0.428	<0.001
Subalpine conifer	-0.206	0.054	-0.367	<0.001	N	n.s.
Aspen	N	n.s.	P	n.s.	N	n.s.

TABLE 211. Variables selected in stepwise regressions of 3 groups of environmental variables against species richness of birds of 3 habitat associations. N = negative association and P = positive association at $P \leq 0.10$. Bolded = selected in the final regression at $P \leq 0.05$ on key variables from each group of environmental variables. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin. Dashes are used where a variable was not selected for a particular habitat group. We did not perform regressions of upland bird species richness on sample unit characteristics and some vegetation characteristics; thus, "n/a" is reported for these pairings.

	Habitat group		
Environmental variable	Aquatic	Riparian–meadow	Upland
Abiotic environment:			
Elevation	**N**	**N**	-
Slope	N	**N**	-
Sample unit characteristics:			
Area	**P**	P	n/a
Depth	-	-	n/a
Bedrock	-	-	n/a
Boulders	N	N	n/a
Cobbles	-	-	n/a
Silt	-	-	n/a
Vegetation characteristics:			
Aquatic plant frequency	-	P	n/a
Logs	N	N	n/a
Canopy cover	-	-	**P**
Wooded riparian	-	**P**	-
Meadow	**P**	**P**	-
Deciduous–coniferous riparian	-	**N**	-
Shrubs	-	N	**P**
Subalpine conifer	N	N	-
Variables in final model	*3*	*5*	*2*
adj. R^2	*0.395*	*0.570*	*0.314*

TABLE 212. Final regression model of key environmental variables related to aquatic bird species richness at lentic sample units (n = 88) in the Lake Tahoe basin. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	P
Elevation	-0.200	0.041	-0.411	-4.910	< 0.001
Area	0.156	0.056	0.235	2.817	0.006
Meadow	3.386	0.616	0.461	5.493	< 0.001

The observed negative relationship between aquatic bird species richness and elevation could be influenced by disturbance at lower elevations. An analysis of covariance with elevation partitioned into 4 groups and road density index as a covariate showed that aquatic bird species richness was not significantly associated with elevation once the influence of disturbance was removed (Table 213). However, with the removal of an outlier (Grass Lake at Luther Pass, with over twice the aquatic bird species richness of any other site), elevation retained its negative relationship with aquatic bird species richness after the influence of disturbance was removed (Table 214).

TABLE 213. Analysis of covariance exploring the relationship between aquatic bird species richness and elevation with road density index as a covariate. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin. SS = sum of squares; ν = degrees of freedom; MS = mean square.

Source of variation	SS	ν	MS	F	*P*
Within + residual	116.14	83	1.40		
Regression	10.70	1	10.70	7.65	0.007
Elevation	5.51	3	1.84	1.31	0.276
Model	30.96	4	7.74	5.53	0.001
Total	147.10	87	1.69		

TABLE 214. Analysis of covariance exploring the relationship between aquatic bird species richness and elevation with road density index as a covariate. Data were collected at lentic sample units (n = 87) in the Lake Tahoe basin. One outlier, Grass Lake at Luther Pass, was removed from the analysis. SS = sum of squares; ν = degrees of freedom; MS = mean square.

Source of variation	SS	ν	MS	F	*P*
Within + residual	68.06	82	0.83		
Regression	3.44	1	3.44	4.14	0.045
Elevation	8.15	3	2.72	3.27	0.025
Model	26.98	4	6.75	8.13	< 0.001
Total	95.05	86			

We examined scatter plots of the 4 environmental variables in the final model against aquatic bird species richness to look for potential environmental thresholds. Three potential thresholds were evident. First, ≤ 1 aquatic bird species were present above 2600 m in elevation and aquatic birds were absent above 2800 m (Fig. 89). Further, 40.6% of units below 2200 m had > 1 aquatic species, while 7.1% of units above 2200 m had > 1 aquatic species, and the number of aquatic species was significantly different between units below and above 2200 m, even with Grass Lake included (U_{88} = 467.0, P = 0.001). Second, aquatic birds were absent at sample units with high log densities (> 46.5% frequency) (Fig. 90). Third, aquatic birds were generally absent at sample units smaller than 0.10 ha and ≤ 2 aquatic birds occurred at sample units smaller than 0.5 ha (Fig. 91).

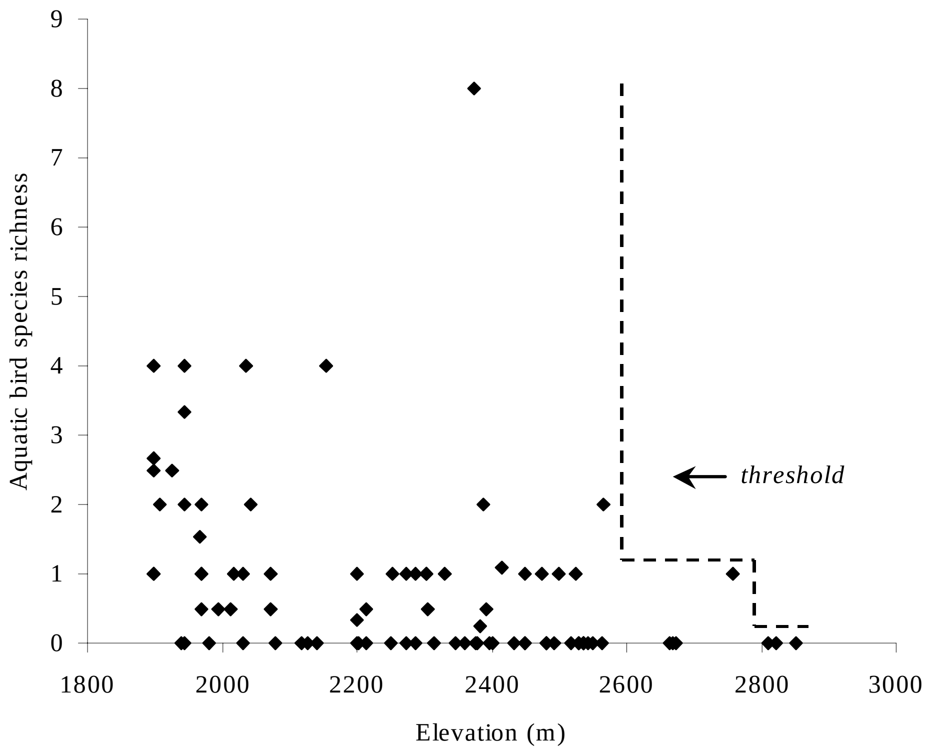


FIG. 89. Relationship of aquatic bird species richness to elevation at 88 lentic sample units in the Lake Tahoe basin.

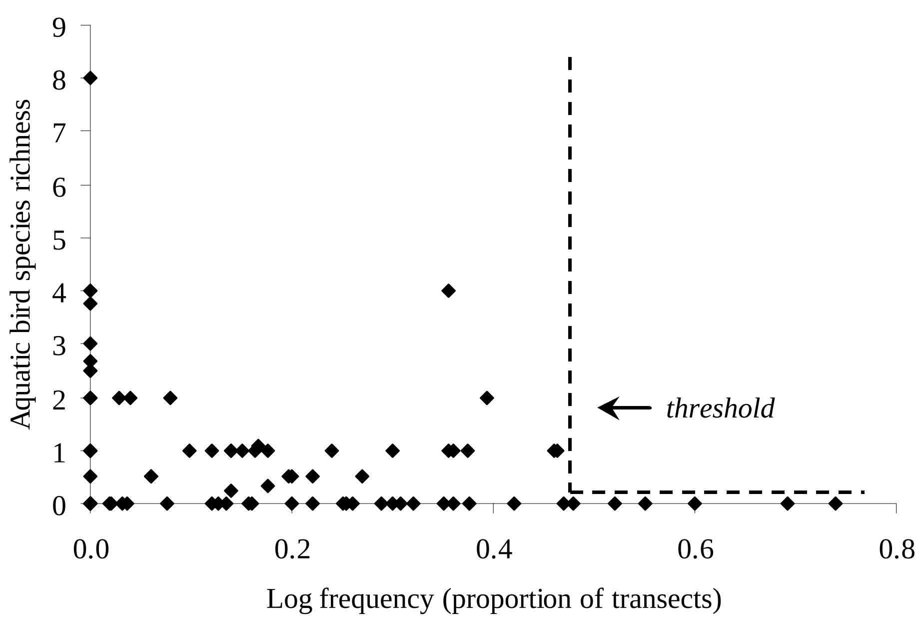


FIG. 90. Relationship of aquatic bird species richness to floating and submerged log frequency at 88 lentic sample units in the Lake Tahoe basin.

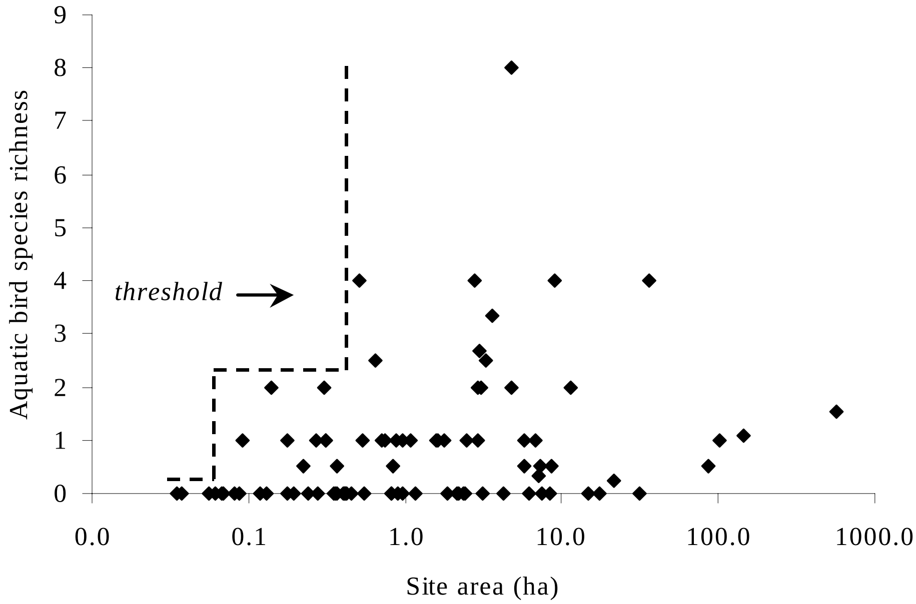


FIG. 91. Relationship of aquatic bird species richness to sample unit area (log scale) at 88 lentic sample units in the Lake Tahoe basin.

Aquatic Bird Species Richness by Basin Orientation. Aquatic bird species richness did not differ by basin orientation (N = 0.5, S = 1.0, E = 1.4, W = 0.5, $\chi^2_{KW} = 5.85$, d.f. = 3, $P = 0.119$).

Correlations with Potential Food Items. Aquatic bird species richness was positively correlated with plant taxonomic richness (r = 0.186, $P = 0.083$) and negatively correlated with caddisfly frequency (r = -0.202, $P = 0.059$).

Regression Model for Riparian–Meadow Bird Species Richness. Riparian–meadow bird species richness was significantly correlated with several environmental variables (Table 210). Regression of riparian–meadow bird species richness on abiotic environmental variables resulted in a 2-variable model: negative associations with elevation and slope (adj. $R^2 = 0.434$; Table 211). Regression of riparian–meadow bird species richness on sample unit variables resulted in a 2-variable model: a positive association with area and a negative association with boulders (adj. $R^2 = 0.129$; Table 211). Regression of riparian–meadow bird species richness on vegetation variables resulted in a 7-variable model: positive associations with plant frequency, wooded riparian, and meadow and negative associations with logs, deciduous–coniferous riparian, shrubs, and subalpine conifer (adj. $R^2 = 0.443$; Table 211). Backward stepwise regression on these 11 key variables resulted in a final 5-variable model: positive associations with wooded riparian and meadow and negative associations with elevation, slope, and deciduous–coniferous riparian ($F_{5,82} = 24.03$, $P < 0.001$, adj. $R^2 = 0.570$; Tables 211 & 215).

TABLE 215. Final regression model of key environmental variables related to riparian–meadow bird species richness at sample lentic sample units (n = 88) in the Lake Tahoe basin. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	*P*
Elevation	-0.313	0.055	-0.461	-5.674	<0.001
Slope	-0.045	0.014	-0.264	-3.192	0.002
Meadow	2.992	0.772	0.292	3.873	0.002
Wooded riparian	2.703	0.926	0.212	2.920	0.005
Deciduous–coniferous riparian	-2.134	0.845	-0.181	-2.525	0.014

The observed negative relationship between riparian–meadow bird species richness and elevation could be influenced by disturbance at lower elevations. An analysis of covariance with elevation partitioned into 4 groups and road density index as a covariate showed that elevation was significantly negatively associated with riparian–meadow bird species richness even after the influence of disturbance was removed (Table 216).

TABLE 216. Analysis of covariance exploring the relationship between riparian–meadow bird species richness and elevation with disturbance (road density) as a covariate. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin. SS = sum of squares; ν = degrees of freedom; MS = mean square.

Source of variation	SS	ν	MS	F	*P*
Within + residual	167.11	83	2.01		
Regression	25.02	1	25.02	12.42	0.001
Elevation	29.39	3	9.80	4.87	0.004
Model	119.20	4	29.80	14.80	<0.001
Total	286.31	87	3.29		

We examined scatter plots of the 5 environmental variables in the final model against riparian–meadow bird species richness to look for potential environmental thresholds. One potential threshold was evident: all sample units > 2600 m in elevation had an average of ≤ 1 riparian–meadow bird species per point count (Fig. 92).

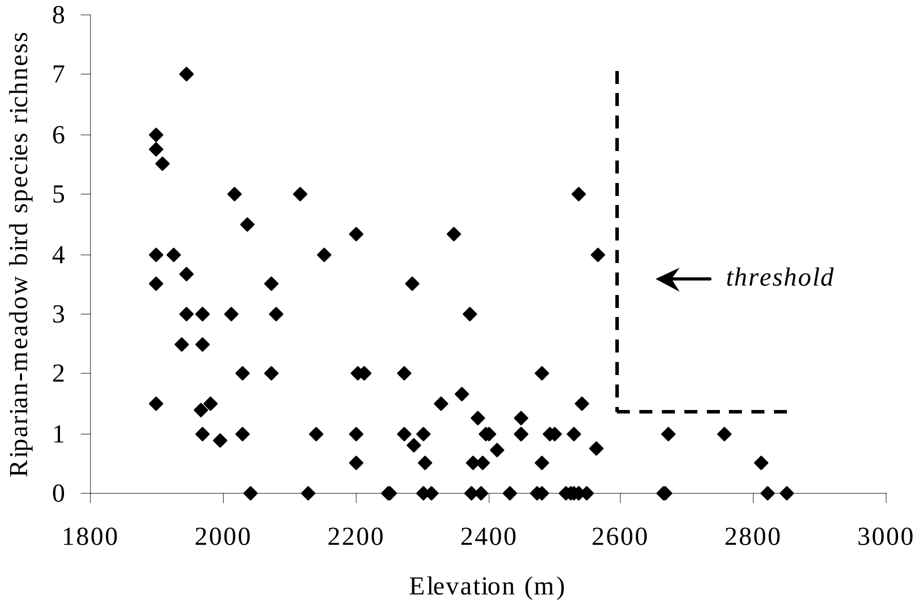


FIG. 92. Relationship of riparian–meadow bird species richness to elevation at 88 lentic sample units in the Lake Tahoe basin.

Riparian–meadow Bird Species Richness by Basin Orientation. Riparian–meadow bird species richness varied significantly by orientation (N = 1.9, S = 1.7, E = 3.4, W = 1.1, χ^2_{KW} = 10.54, d.f. = 3, P = 0.015) and was greater on the east side than on the south and west sides of the basin based on multiple comparison tests.

Regression Model for Upland Bird Species Richness. Upland bird species richness was significantly correlated with several environmental variables (Table 210). Regression of upland bird species richness on abiotic environmental variables resulted in no variables being selected (Table 211). Regression of upland bird species richness on sample unit variables also resulted in no variables being selected (Table 211). Regression of upland bird species richness on vegetation variables resulted in a 2-variable model: positive associations with canopy cover and shrubs (adj. R^2 = 0.314; Table 211). Backward stepwise regression on these 2 key variables resulted in both variables being retained ($F_{2,85}$ = 20.94, P < 0.001, adj. R^2 = 0.314; Tables 211 & 217).

TABLE 217. Final regression model of key environmental variables related to upland bird species richness at sample lentic sample units (n = 88) in the Lake Tahoe basin. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	P
Canopy cover	0.095	0.015	0.588	6.361	<0.001
Shrubs	3.313	1.136	0.270	2.918	0.005

We examined scatter plots of the 2 environmental variables in the final model against upland bird species richness to look for potential environmental thresholds. No potential thresholds were evident.

Upland Bird Species Richness by Basin Orientation. Upland bird species richness did not vary by basin orientation (ANOVA; N = 8.3, S = 8.6, E = 7.5, W = 8.3, $F_{3,84}$ = 0.51, P = 0.678).

Correlations with Environmental Gradients. Aquatic, riparian–meadow, and upland bird species richness and were significantly correlated with several environmental gradients (Table 218). Aquatic and riparian–meadow bird species richness were both negatively correlated with the elevation–precipitation and the bedrock–boulders gradient. Aquatic bird species richness also was higher with greater proportions of surrounding meadow as opposed to aspen. Riparian–meadow bird species richness was higher at silty units and lower in units surrounded by subalpine vegetation. Upland bird species richness was greater with an abundance of riparian vegetation and lower with an abundance of subalpine vegetation.

TABLE 218. Significant correlations between bird species richness in 3 habitat groups and environmental gradients. Data were collected at 88 lentic sample units in the Lake Tahoe basin.

Environmental gradient	r	*P*
Aquatic birds:		
Bedrock–boulders	-0.212	0.048
Elevation–precipitation	-0.460	<0.001
Aspen to meadow	-0.244	0.022
Riparian–meadow birds:		
Sand to silt	0.241	0.024
Bedrock–boulders	-0.353	0.001
Elevation–precipitation	-0.659	<0.001
Subalpine vegetation	-0.347	0.001
Upland birds:		
Riparian vegetation	0.290	0.006
Subalpine vegetation	-0.224	0.036

Patterns of Bird Abundance by Habitat Association

Environmental Relationships of Habitat Groups

Regression Model for Aquatic Bird Abundance. Aquatic bird abundance was significantly correlated with several environmental variables (Table 219). Regression of aquatic bird abundance on abiotic environmental variables resulted in a 1-variable model: a negative association with precipitation (adj. $R^2 = 0.076$; Table 220). Regression of aquatic bird abundance on sample unit variables resulted in a 2-variable model: a positive association with area and a negative association with cobbles (adj. $R^2 = 0.134$; Table 219). Regression of aquatic bird abundance on vegetation variables resulted in a 3-variable model: a positive association with meadow and negative associations with logs and shrubs (adj. $R^2 = 0.183$; Table 220). Backward stepwise regression on these 6 key variables resulted in a final 4-variable model: positive associations with area and meadow and negative associations with precipitation and shrubs ($F_{4,83} = 10.14$, $P < 0.001$, adj. $R^2 = 0.296$; Tables 220 & 221).

TABLE 219. Significant ($P \leq 0.10$) correlations between average abundance of 3 bird groups and 25 environmental variables. N and P indicate non-significant (n.s.) negative and positive correlations, respectively. We did not calculate correlations between sample unit characteristics, some vegetation characteristics, and upland bird abundance; thus, "n/a" is reported for these pairings.

	Habitat group					
	Aquatic		Riparian–meadow		Upland	
Environmental variable	r	*P*	r	*P*	r	*P*
Abiotic environment:						
Elevation	-0.225	0.035	-0.526	<0.001	N	n.s.
Precipitation	-0.294	0.005	-0.524	<0.001	N	n.s.
Slope	-0.235	0.028	-0.488	<0.001	N	n.s.
Sample unit characteristics:						
Area	0.308	0.004	P	n.s.	n/a	n/a
Perimeter	0.326	0.002	0.188	0.079	n/a	n/a
Depth	P	n.s.	N	n.s.	n/a	n/a
Bedrock	N	n.s.	-0.183	0.088	n/a	n/a
Boulders	N	n.s.	-0.262	0.014	n/a	n/a
Cobbles	N	n.s.	N	n.s.	n/a	n/a
Pebbles	N	n.s.	N	n.s.	n/a	n/a
Sand	P	n.s.	P	n.s.	n/a	n/a
Silt	P	n.s.	P	n.s.	n/a	n/a
Vegetation characteristics:						
Logs	-0.314	0.003	-0.426	<0.001	n/a	n/a
Overhanging vegetation	-0.213	0.046	N	n.s.	n/a	n/a
Aquatic plant diversity	P	n.s.	0.414	<0.001	n/a	n/a
Aquatic plant frequency	P	n.s.	0.305	0.004	n/a	n/a
Canopy cover	P	n.s.	N	n.s.	0.355	0.001
Wooded riparian	N	n.s.	P	n.s.	P	n.s.
Meadow	0.309	0.003	0.368	<0.001	P	n.s.
Deciduous–coniferous riparian	N	n.s.	-0.252	0.018	P	n.s.
Shrubs	-0.238	0.025	N	n.s.	P	n.s.
Mixed conifer	P	n.s.	P	n.s.	0.308	0.003
Subalpine conifer	N	n.s.	-0.311	0.003	P	n.s.
Aspen	N	n.s.	P	n.s.	N	n.s.

TABLE 220. Variables selected in stepwise regressions of 3 groups of environmental variables against average abundance of birds of 3 habitat associations. N = negative association and P = positive association at $P \leq 0.10$. Bolded = selected in the final regression at $P \leq 0.05$ on key variables from each group of environmental variables. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin. Dashes are used where a variable was not selected for a particular habitat group. We did not perform regressions of upland bird abundance on sample unit characteristics and some vegetation characteristics; thus, "n/a" is reported for these pairings.

	Habitat group		
Environmental variable	Aquatic	Riparian–meadow	Upland
Abiotic environment:			
Elevation	-	**N**	-
Precipitation	**N**	N	-
Slope	-	**N**	-
Sample unit characteristics:			
Area	**P**	N	-
Depth	-	-	n/a
Boulders	-	N	n/a
Cobbles	N	-	n/a
Pebbles	-	-	n/a
Vegetation characteristics:			
Aquatic plant frequency	-	P	n/a
Logs	N	**N**	n/a
Overhanging vegetation	-	-	n/a
Canopy cover	-	-	**P**
Aspen	-	**P**	-
Meadow	**P**	**P**	-
Deciduous–coniferous riparian	-	**N**	-
Shrubs	**N**	-	**P**
Subalpine conifer	-	N	-
Variables in final model	*4*	*6*	*2*
adj. R^2	*0.296*	*0.549*	*0.211*

TABLE 221. Final regression model of key environmental variables related to aquatic bird abundance at sample lentic sample units (n = 88) in the Lake Tahoe basin. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	P
Precipitation	-0.054	0.017	-0.288	-3.193	0.002
Meadow	10.202	3.160	0.291	3.228	0.002
Area	0.977	0.287	0.308	3.405	0.001
Shrubs	-6.792	2.480	-0.248	-2.738	0.008

The observed relationship between aquatic bird abundance and precipitation could be influenced by disturbance at sites with lower precipitation. An analysis of covariance with precipitation partitioned into 4 groups and road density as a covariate showed that precipitation was significantly negatively associated with aquatic bird abundance even after the influence of disturbance was removed (Table 222).

TABLE 222. Analysis of covariance exploring the relationship between aquatic bird abundance and precipitation with disturbance (road density) as a covariate. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin. SS = sum of squares; ν = degrees of freedom; MS = mean square.

Source of variation	SS	ν	MS	F	*P*
Within + residual	2749.80	83	33.13		
Regression	11.87	1	11.87	0.36	0.551
Precipitation	411.40	3	137.13	4.14	0.009
Model	593.48	4	148.37	4.48	0.003
Total	3343.28	87	38.43		

We examined scatter plots of the 4 environmental variables in the final model against aquatic bird abundance to look for potential environmental thresholds. One potential threshold was evident: sample units with > 120 cm of precipitation annually had ≤ 5 aquatic birds per point count, and sample units with > 140 cm of precipitation had ≤ 2 aquatic birds per point count (Fig. 93).

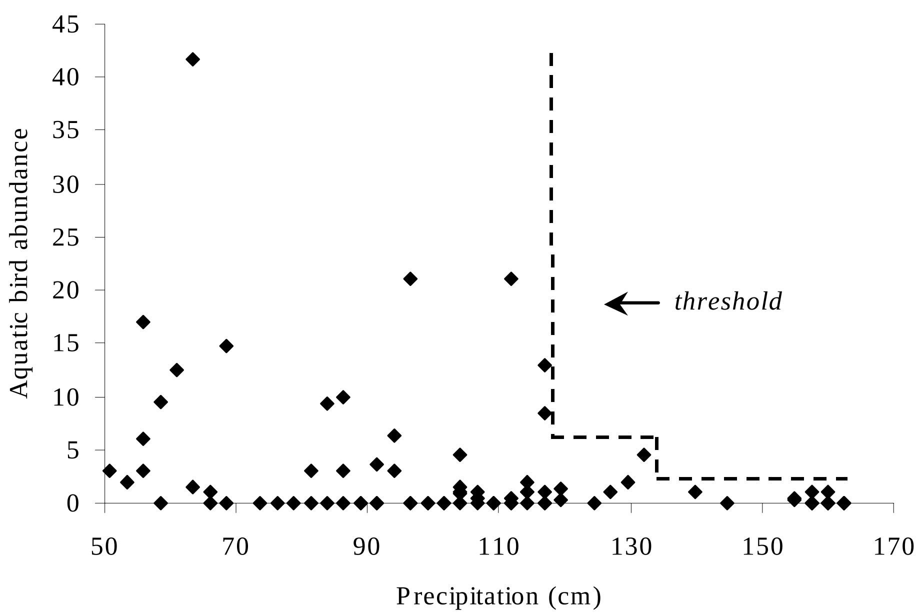


FIG. 93. Relationship of annual precipitation to aquatic bird abundance at 88 lentic sample units in the Lake Tahoe basin.

Aquatic Bird Abundance by Basin Orientation. Aquatic bird abundance was not significantly different among the 4 basin orientations (N = 1.5, S = 3.1, E = 7.2, W = 0.7, χ^2_{KW} = 6.84, P = 0.077), but it was greater on the east side than on the west side of the basin in multiple comparison tests.

Correlations with Potential Food Items. Aquatic bird abundance was negatively correlated with caddisfly frequency (r = -0.222, P = 0.038).

Regression Model for Riparian–Meadow Bird Abundance. Riparian–meadow bird abundance was significantly correlated with several environmental variables (Table 219). Regression of riparian–meadow bird abundance on abiotic environmental variables resulted in a 3-variable model: negative associations with elevation, precipitation, and slope (adj. $R^2 = 0.379$; Table 220). Regression of riparian–meadow bird abundance on sample unit variables resulted in a 2-variable model: a positive association with area and a negative association with boulders (adj. $R^2 = 0.095$; 220). Regression of riparian–meadow bird abundance on vegetation variables resulted in a 6-variable model: positive associations with plant frequency, aspen, and meadow and negative associations with logs, deciduous–coniferous riparian, and subalpine conifer (adj. $R^2 = 0.391$; Table 220). Backward stepwise regression on these 11 variables resulted in a final 6-variable model: positive associations with aspen and meadow and negative associations with elevation, slope, deciduous–coniferous riparian, and logs ($F_{6,81} = 18.67$, $P < 0.001$, adj. $R^2 = 0.549$; Tables 220 & 223).

TABLE 223. Final regression model of key environmental variables related to riparian–meadow bird abundance at sample lentic sample units (n = 88) in the Lake Tahoe basin. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	*P*
Aspen	183.227	81.895	0.166	2.237	0.028
Deciduous–coniferous riparian	-11.110	3.806	-0.211	-2.919	0.005
Meadow	15.029	3.614	0.329	4.158	0.001
Logs	-5.401	2.402	-0.176	-2.249	0.027
Elevation	-1.187	0.258	-0.392	-4.601	<0.001
Slope	-0.168	0.065	-0.223	-2.586	0.012

The observed relationship between riparian–meadow bird abundance and elevation could be influenced by disturbance at lower elevations. An analysis of covariance with elevation partitioned into 4 groups and road density as a covariate showed that the relationship of elevation to riparian–meadow bird abundance disappeared once the influence of disturbance was removed (Table 224).

TABLE 224. Analysis of covariance exploring the relationship between riparian–meadow bird abundance and elevation with road density index as a covariate. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin. SS = sum of squares; ν = degrees of freedom; MS = mean square.

Source of variation	SS	ν	MS	F	*P*
Within + residual	2836.43	83	34.17		
Regression	1018.78	1	1018.78	29.81	< 0.001
Elevation	181.30	3	60.43	1.77	0.160
Model	2846.97	4	711.74	20.83	< 0.001
Total	5683.40	87	65.33		

We examined scatter plots of the 6 environmental variables in the final model against riparian–meadow bird abundance to look for potential environmental thresholds. No potential thresholds were evident.

Riparian–meadow Bird Abundance by Basin Orientation. Riparian–meadow bird abundance was significantly different among the 4 basin orientations (N = 4.4, S = 4.3, E = 14.5, W = 1.8, $\chi^2_{KW} = 12.35$, $P = 0.006$) and was greater on the east side than on all other sides of the basin based on multiple comparison tests.

Regression Model for Upland Bird Abundance. Upland bird abundance was significantly correlated with two environmental variables (Table 219). Regression of upland bird abundance on abiotic environmental variables resulted in no variables being selected. Regression of upland bird abundance on vegetation variables resulted in a 2-variable model: positive associations with canopy cover and shrubs (adj. $R^2 = 0.149$; Table 220). Backward stepwise regression resulted in the 2 variables being retained ($F_{2,85} = 8.61$, $P < 0.001$, adj. $R^2 = 0.149$; Tables 220 & 225).

TABLE 225. Final regression model of key environmental variables related to upland bird abundance at sample lentic sample units (*n* = 88) in the Lake Tahoe basin. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	*P*
Canopy cover	0.135	0.034	0.415	4.027	<0.001
Shrubs	5.341	2.559	0.215	2.087	0.040

We examined scatter plots of the 2 environmental variables in the final model against upland bird abundance to look for potential environmental thresholds. No potential thresholds were evident.

Upland Bird Abundance by Basin Orientation. Upland bird abundance was marginally significantly different among basin orientations (ANOVA; N = 19.1, S = 15.6, E = 13.3, W = 15.3, $F_{3,84} = 2.43$, $P = 0.071$) and was greater on the north side than on the east side of the basin based on multiple comparison tests.

Correlations with Environmental Gradients. Correlations of bird abundance by habitat group with environmental gradients are reported in Table 226. Aquatic and riparian–meadow bird abundance were significantly correlated with several environmental gradients, again sharing a negative relationship with the elevation–precipitation gradient. Aquatic bird abundance was also positively associated with the sample unit area gradient, and negatively associated with the aspen to meadow gradient. Riparian–meadow bird abundance was negatively related to two elevation-associated gradients: the bedrock–boulders and subalpine vegetation gradients. Upland bird abundance was not correlated with any environmental gradient.

TABLE 226. Significant correlations between bird abundance and environmental gradients. Data are from 88 lentic sample units in the Lake Tahoe basin.

Environmental gradient	r	*P*
Aquatic:		
Sample unit area	0.208	0.051
Elevation–precipitation	-0.346	0.001
Aspen to meadow	-0.236	0.027
Riparian–meadow:		
Bedrock–boulders	-0.312	0.003
Elevation–precipitation	-0.634	<0.001
Subalpine vegetation	-0.222	0.038
Upland:		
None		

Summary of Results of Bird Alpha Diversity Relationships

We observed several consistent patterns of association of bird species richness and abundance with environmental variables. Species richness and abundance exhibited similar relationships with environmental variables in nearly all cases. Generally, bird species richness and abundance were negatively associated with elevation, precipitation, slope, and subalpine vegetation and positively associated with meadow vegetation with the exceptions of upland bird species richness and abundance. The 3 habitat groups were associated differently with most other environmental variables.

Seven environmental variables showed trends in their relationships with bird habitat groups (Table 227). Elevation, precipitation, and slope had their maximum influence over riparian–meadow birds, with secondary influence over aquatic birds and no significant influence over upland birds. Riparian vegetation, mixed conifer, and canopy cover were most influential over upland birds, while meadow most strongly affected aquatic birds.

TABLE 227. Summary of regression relationships between bird habitat groups and environmental variables that showed a gradient of change from aquatic to upland birds. Thicker parts of the bars represent greater influence. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin.

	Bird habitat group		
Environmental variables	Aquatic	Riparian–meadow	Upland
Abiotic environment:		Elevation	
		Precipitation	
		Slope	
Vegetation characteristics:		Riparian vegetation	
		Mixed conifer	
		Canopy cover	
		Meadow	

Patterns of Amphibian Diversity

General Patterns

A total of 5 amphibian species were detected (see Chapter 12, Table 5). The richness of native amphibian species ranged from 0 to 3 ($\bar{x}$ = 0.66, SE = 0.08) across sample units (Appendix 23). Skinny Whale Pond and Edgewood Lake each had 3 amphibian species, and 8 sample units had 2 amphibian species.

Environmental Relationships of Amphibian Species Richness

Regression Model for Amphibian Species Richness

Amphibian species richness was significantly correlated ($P \leq 0.10$) with 4 environmental variables (Table 228). Regression of amphibian species richness on abiotic environmental variables resulted in no variables being selected. Regression on sample unit variables resulted in a 1-variable model: a negative association with cobbles ($F_{1,86}$ = 5.842, P = 0.018, adj. R^2 = 0.053) (Table 229). Regression on vegetation variables resulted in no variables being selected. The final model consisted of the negative relationship with cobbles and explained little of the variation in amphibian species richness (Table 229, Table 230).

TABLE 228. Significant correlations of amphibian species richness with environmental variables at 88 lentic sample units in the Lake Tahoe basin.

Environmental variable	r	*P*
Silt	0.182	0.089
Depth	-0.212	0.048
Boulders	-0.188	0.080
Cobbles	-0.299	0.005

TABLE 229. Variables selected in stepwise regressions of 3 groups of environmental variables and amphibian species richness. N = negative association and P = positive association at $P \leq 0.10$. Bolded = selected in the final regression at $P \leq 0.05$ on key variables from each group of environmental variables. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin.

Environmental variables	Amphibian species richness
Sample unit characteristics:	
Cobbles	**N**
Variables in final model	*1*
adj. R^2	*0.053*

TABLE 230. Final regression model of key environmental variables related to amphibian species richness at sample lentic sample units (n = 88) in the Lake Tahoe basin. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	*P*
Cobbles	-0.951	0.394	-0.252	-2.417	0.018

A graph of cobbles against amphibian species richness revealed a potential environmental threshold (Fig. 94). No amphibians occurred at sample units where the substrate was ≥ 20% cobbles.

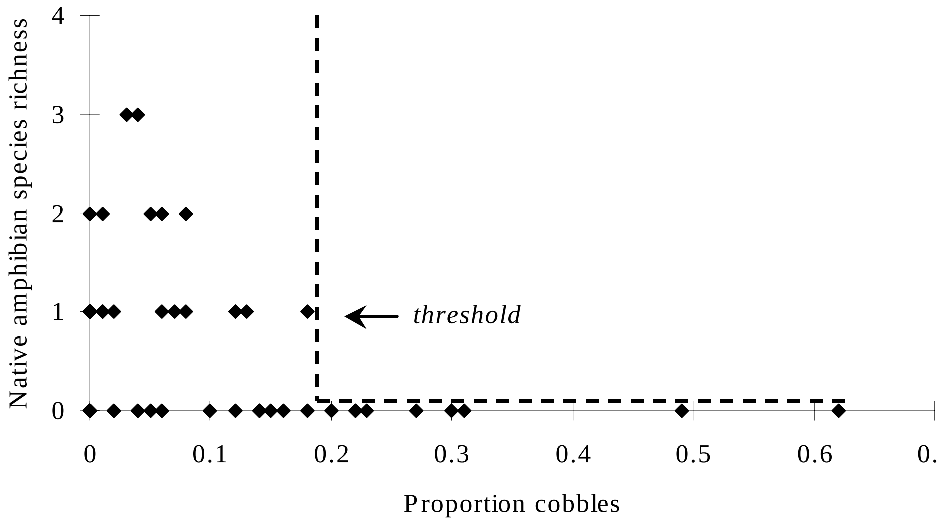


FIG. 94. Relationship between proportion of cobbles in substrate and native amphibian species richness at lentic sample units (n = 88) in the Lake Tahoe basin.

Amphibian Species Richness and Predatory Fish

Amphibian species richness was not significantly different between sample units with trout and sample units without trout (t_{86} = 0.61, P = 0.546).

Amphibian Species Richness by Basin Orientation

Amphibian species richness did not vary by basin orientation (ANOVA; N = 0.7, S = 0.5, E = 0.9, W = 0.7, $F_{3,84}$ = 0.96, P = 0.416).

Correlations with Environmental Gradients

Amphibian species richness was not significantly correlated with any of the environmental gradients.

Patterns of Littoral Zone Plant Diversity

General Patterns

A total of 59 littoral zone plant taxa were detected (Appendix 24). Plant taxonomic richness ranged from 0 to 4.82 per sample unit ($\bar{x}$ = 1.35, SE = 0.11; Appendix 23). General Creek Meadow had the highest plant taxonomic richness (4.82), followed by Folsom Spring Pond (4.36) and Wildwood Basin (3.62). Plant frequency ranged from 0% to 100% of transects per sample unit ($\bar{x}$ = 74%, SE = 0.03). Thirty sample units had plants in 100% of transects. Plant taxonomic richness and frequency were highly positively correlated (r = 0.724, P < 0.001) (Fig. 95); thus, taxonomic richness was highest where plants occurred more frequently.

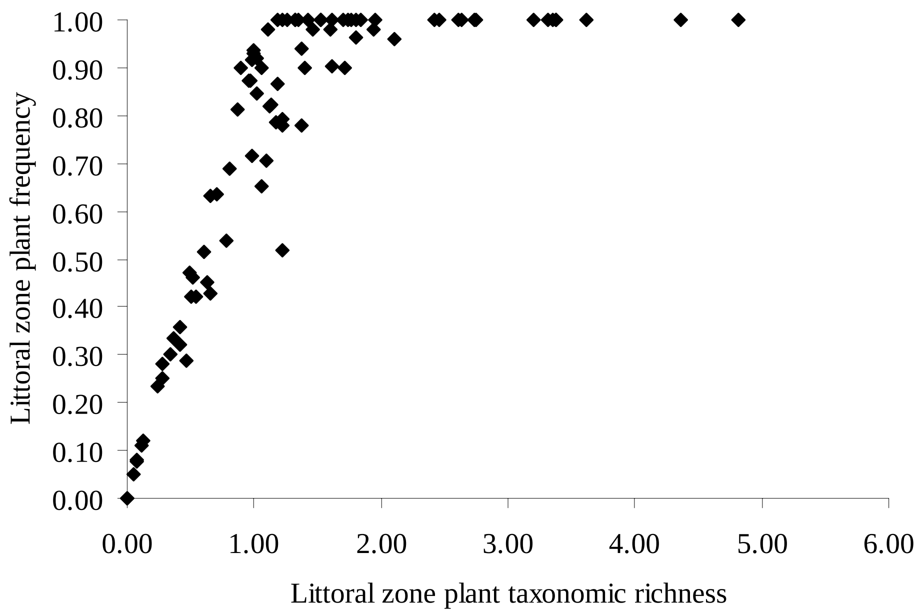


FIG. 95. Relationship of littoral zone plant frequency to taxonomic richness at 88 lentic sample units in the Lake Tahoe basin.

Environmental Relationships of Plant Taxonomic Richness

Regression Model for Plant Taxonomic Richness

Plant taxonomic richness was significantly correlated ($P \leq 0.10$) with several environmental variables (Table 231). Regression of plant taxonomic richness on abiotic environmental variables resulted in a 1-variable model: a negative association with elevation (adj. $R^2 = 0.038$; Table 232). Three sample unit variables, area, perimeter, and sand, were negatively correlated with richness but loaded in the regression model with positive relationships; they were therefore dropped from consideration in the model. Regression of plant taxonomic richness on the remaining sample unit variables resulted in a 2-variable model: a positive association with silt and a negative association with boulders (adj. $R^2 = 0.504$; Table 232). Regression of plant taxonomic richness on vegetation variables resulted in a 4-variable model: positive associations with canopy cover, meadow, and wooded riparian, and a negative association with logs (adj. $R^2 = 0.193$; Table 232). Backward stepwise regression on these 7 key variables resulted in a final 2-variable model: a positive association with silt and a negative association with logs ($F_{2,85} = 53.71$, $P < 0.001$, adj. $R^2 = 0.548$; Tables 232 & 233).

TABLE 231. Significant correlations of littoral zone plant taxonomic richness with environmental variables at 88 lentic sample units in the Lake Tahoe basin.

Environmental variable	r	*P*
Silt	0.610	<0.001
Wooded riparian	0.311	0.003
Deciduous–coniferous riparian	0.207	0.054
Meadow	0.287	0.007
Elevation	-0.221	0.038
Area	-0.213	0.047
Perimeter	-0.213	0.046
Depth	-0.345	0.001
Bedrock	-0.276	0.009
Boulders	-0.436	<0.001
Cobbles	-0.388	<0.001
Pebbles	-0.197	0.066
Sand	-0.338	0.001
Logs	-0.299	0.005

TABLE 232. Variables selected in stepwise regressions of 3 groups of environmental variables and littoral zone plant taxonomic richness. N = negative association and P = positive association at $P \leq 0.10$. Bolded = selected in the final regression at $P \leq 0.05$ on key variables from each group of environmental variables. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin.

Environmental variable	Aquatic plant diversity
Abiotic environment:	
Elevation	N
Sample unit characteristics:	
Silt	**P**
Boulders	N
Vegetation characteristics:	
Canopy cover	P
Meadow	P
Wooded riparian	P
Logs	**N**
Variables in final model	*2*
adj. R^2	*0.452*

TABLE 233. Final regression model of key environmental variables related to littoral zone plant taxonomic richness at lentic sample units (n = 88) in the Lake Tahoe basin. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	*P*
Silt	1.138	0.153	0.593	7.427	<0.001
Logs	-1.066	0.303	-0.280	-3.512	0.001

We examined scatter plots of plant taxonomic richness against the 2 environmental variables in the final regression model to elucidate potential environmental thresholds. No thresholds were evident.

Plant Taxonomic Richness by Basin Orientation

Plant taxonomic richness did not vary by basin orientation (ANOVA; N = 1.1, S = 1.3, E = 1.8, W = 1.3, $F_{3,84} = 1.12$, $P = 0.347$).

Correlations with Environmental Gradients

Plant taxonomic richness was significantly correlated with several environmental gradients (Table 234). Richness was higher with greater amounts of riparian vegetation and lower at higher elevations, at larger sample units, and with greater amounts of aspen as opposed to meadow.

TABLE 234. Significant correlations of littoral zone plant taxonomic richness with environmental gradients at 88 lentic sample units in the Lake Tahoe basin.

Environmental gradient	r	*P*
Riparian vegetation	0.234	0.028
Elevation–precipitation	-0.260	0.014
Sample unit area	-0.292	0.006
Aspen to meadow	-0.186	0.082

Environmental Relationships of Littoral Zone Plant Frequency

Regression Model for Plant Frequency

Plant frequency was significantly correlated ($P \leq 0.10$) with several environmental variables (Table 235). Regression of plant frequency on abiotic environmental variables resulted in a 1-variable model: a negative association with elevation (adj. $R^2 = 0.032$; Table 236). Regression of plant frequency on sample unit variables resulted in a 2-variable model: a positive association with silt and a negative association with boulders (adj. $R^2 = 0.656$; Table 236). We omitted mixed conifer from consideration in the vegetation model due to an inconsistent relationship with the dependent variable. Regression of plant frequency on the remaining vegetation variables resulted in a 3-variable model: positive associations with wooded riparian, meadow, and deciduous–coniferous riparian (adj. $R^2 = 0.215$; Table 236). Backward stepwise regression on the 6 key variables resulted in a 2-variable model: a positive association with silt and a negative association with boulders ($F_{2,85} = 83.91$, $P < 0.001$, adj. $R^2 = 0.656$; Tables 236 & 237).

TABLE 235. Significant correlations of littoral zone plant frequency with environmental variables at 88 lentic sample units in the Lake Tahoe basin.

Environmental variable	r	*P*
Silt	0.810	<0.001
Canopy cover	0.195	0.069
Wooded riparian	0.345	0.001
Deciduous–coniferous riparian	0.263	0.013
Meadow	0.226	0.034
Mixed conifer	0.184	0.086
Elevation	-0.209	0.050
Area	-0.346	0.001
Perimeter	-0.367	<0.001
Depth	-0.519	<0.001
Bedrock	-0.339	0.001
Boulders	-0.604	0.001
Cobbles	-0.545	<0.001
Pebbles	-0.209	0.051
Sand	-0.449	<0.001

TABLE 236. Variables selected in stepwise regressions of 3 groups of environmental variables and littoral zone plant frequency. N = negative association and P = positive association at $P \leq 0.10$. Bolded = selected in the final regression at $P \leq 0.05$ on key variables from each group of environmental variables. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin.

Environmental variables	Littoral zone plant frequency
Abiotic environment:	
Elevation	**N**
Sample unit characteristics:	
Silt	**P**
Boulders	**N**
Vegetation characteristics:	
Wooded riparian	**P**
Meadow	P
Deciduous–coniferous riparian	P
Variables in final model	2
adj. R^2	*0.656*

TABLE 237. Final regression model of key environmental variables related to littoral zone plant frequency at sample lentic sample units (n = 88) in the Lake Tahoe basin. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	*P*
Silt	0.377	0.055	0.620	6.907	<0.001
Boulders	-0.356	0.129	-0.247	-2.751	0.007

The observed relationship between plant frequency and elevation could be influenced by disturbance being higher at lower elevations. An analysis of covariance with elevation partitioned into 4 groups and road density as a covariate showed that elevation was significantly associated with plant frequency even after the influence of disturbance was removed (Table 238).

TABLE 238. Analysis of covariance exploring the relationship between littoral zone plant frequency and elevation with road density index as a covariate. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin. SS = sum of squares; ν = degrees of freedom; MS = mean square.

Source of variation	SS	ν	MS	F	P
Within + residual	780.53	83	9.40		
Regression	84.82	1	84.82	9.02	0.004
Elevation	284.60	3	94.87	10.09	<0.001
Model	412.24	4	103.06	10.96	<0.001
Total	1192.76	87	13.71		

We examined scatter plots of plant frequency against the 2 environmental variables in the final regression model to elucidate potential environmental thresholds. No thresholds were evident.

Plant Frequency by Basin Orientation

Plant frequency was nearly identical across basin orientations and did not differ statistically (N = 0.76, S = 0.74, E = 0.75, W = 0.73, $F_{3,84}$ = 0.028, P = 0.994).

Correlations with Environmental Gradients

Plant frequency was positively correlated with the riparian vegetation gradient (r = 0.307, P = 0.004) and negatively correlated with the elevation–precipitation gradient (r = -0.217, P = 0.042) and the area gradient (r = -0.386, P < 0.001).

DISCUSSION

Environmental Characteristics

The 1000-m range in elevation we sampled represented a significant gradient in environmental conditions. Higher elevation is generally associated with declines in mean temperature and greater extreme low temperature, increasing precipitation (falling increasingly as snow at higher elevations), steeper slopes, shorter growing seasons, and higher winds (Whittaker 1975, Smith et al. 1990, Nikilov and Zeller 1992, Dahlgren et al. 1997). These changing conditions along the elevational gradient limit the occurrence of many animals and plants. The observed declines in many measures of diversity from low to high elevations (see below) are likely the result of many environmental factors associated with higher elevations.

One such factor is the terrestrial vegetation surrounding the lentic unit. (Vegetation types and their contributions to biological diversity are treated more fully in Chapter 4.) The primary vegetation gradient associated with lentic sample units reflected the influence of elevation, from mixed conifer at lower elevations to subalpine conifer forest and shrubs at higher elevations. Vegetation changes along the elevation gradient are likely to be accompanied by significant biotic variation, as species turnover may be triggered by changes in vegetation types (Whittaker 1975).

The gradient of aspen to meadow represented the second vegetation gradient surrounding lentic ecosystems even though aspen was the least common vegetation type. Aspen and meadow are unique and uncommon ecosystems that require slightly different soil moisture regimes. Both ecosystems require moist soils, with aspen ecosystems forming in areas with high but subsurface water tables (Verner 1988) and meadows forming in flatter areas with water tables at or near the surface (Ratliff 1988). Thus, the two ecosystems tend not to co-occur. The important contribution of these relatively rare ecosystems to a diversity of vegetation types in the basin is highlighted here. Both ecosystems are known to support a diversity of fauna and flora that may not occur elsewhere.

A wide variety of substrate types was observed, indicating the potential for a range of productivity of lentic units and available habitat elements. Substrate may influence the occurrence and abundance of a variety of taxa. For instance, aquatic plant growth is favored in silt conditions (Goldman and Horne 1983), a pattern exhibited in this study by the positive association of plant diversity and frequency with silt in the PCA and in regression analyses. Plants in turn support a diversity of many other taxa. Many aquatic invertebrates rely on plants for food, cover, and egg-laying substrate (Caduto 1990), some birds use them for food and cover (Ehrlich et al. 1988), and amphibians often use them as cover and anchors for egg masses (Zeiner et al. 1988). Certain substrate types may provide important habitat elements for aquatic biota. Rocky substrates, for instance, supply fish with cover (Moyle 1976), thereby affecting the occurrence of piscivorous animals, such as garter snakes and some waterfowl. Thus, although lentic units dominated by silt are more productive than rocky lentic units, those dominated by rocky substrates support a distinct fauna.

Overhanging vegetation and floating and submerged logs provide cover for amphibians, invertebrates, and potentially many other aquatic organisms. Both were highly variable among lentic units, indicating a range of available cover for aquatic biota. The overhanging vegetation we observed was composed primarily of woody riparian plants, such as willows and alders. Riparian vegetation, therefore, in addition to representing habitat for terrestrial animals, may provide important cover for aquatic animals as well. Logs are another element of cover in lentic ecosystems that are a direct result of surrounding vegetation conditions. Lentic ecosystems surrounded by forests will tend to have more logs to provide cover for invertebrates and amphibians.

Several environmental characteristics varied among the 4 basin orientations. The sample results reflected the dominant patterns of environmental variation around the basin; thus, the sample should also reflect biotic responses to these patterns, manifested as differences in diversity among basin orientations. The west side of the basin was characterized by steeper, rockier terrain with a greater range of elevations and precipitation than the other sides of the basin. Due to the importance of elevation, precipitation, and slope in explaining variation in environmental characteristics, the west side should exhibit a greater range in biological diversity than the other sides of the basin. The east side was generally more disturbed than other sides of the basin, suggesting that effects of disturbance on biological diversity will be displayed the most profoundly on the east side. In addition, mayflies were more frequent in the east, while caddisflies were more frequent in the west. The north and south sides of the basin were usually intermediate in environmental characteristics, so inasmuch as the environmental characteristics we measured explain biological diversity, these basin orientations will likely be intermediate in biological diversity as well.

Patterns of Bird Diversity

Lentic ecosystems in the Lake Tahoe basin provide habitat for a variety of bird species—a total of 93 native species were detected, with nearly 45% of these primarily associated with aquatic, riparian, and meadow ecosystems. It is clear that lakes, ponds, and wet meadows provide vital habitat for birds in the basin. As many of the environmental influences on bird diversity were similar in lentic and lotic ecosystems, readers are referred to Chapter 5 for a broader discussion of the management of meadows and riparian vegetation and the implications of higher diversity at low elevations in the basin. Here we discuss the implications of the observed patterns of bird diversity for the conservation and management of the basin's lentic ecosystems.

Bird diversity was closely related to terrestrial vegetation surrounding lentic sample units. Generally, bird diversity was higher in association with riparian and meadow vegetation, but unique patterns of association were observed among bird habitat groups. Aquatic bird diversity increased near meadow vegetation. Aquatic birds may forage primarily in the aquatic environment, but they generally nest in the upland environment adjacent to lentic units. For example, Mallards often nest in tall grasses near water (Ehrlich et al. 1988), and Killdeer and Spotted Sandpipers nest in open habitats including meadows (Swarth 1990a, 1990b). Thus, the presence of meadows suitable for breeding by aquatic birds may influence their occurrence at lentic units. Riparian–meadow birds were more diverse near meadows, riparian vegetation, and aspen, ecosystems that are known to support a wide variety of bird species (Graber 1996, Schlesinger and Holst 2000). Areas in the basin with greater amounts of riparian vegetation appear to play an important role in supporting bird species richness.

Upland birds showed somewhat different patterns of diversity. Though upland birds were also associated with riparian vegetation, their associations were stronger with shrubs and canopy cover. Canopy cover is an important component of habitat for songbirds (Ryder 1986), which comprised a majority of the birds in the upland group. Canopy cover provides protection from predators and the elements and supports increased upland bird diversity in the basin. Upland birds were also more diverse in shrublands, a finding that indicates that a variety of upland habitats, those with canopy cover and without, is important for bird diversity. The fact that shrubs were more prevalent at high elevations suggests that elevation does not negatively affect upland birds to the extent it affects aquatic and riparian–meadow birds. This idea is reinforced by direct relationships with elevation, discussed below.

The negative relationship observed between elevation and the alpha diversity of all birds suggests that diversity was lower in the harsh conditions (e.g., high winds, low temperatures) at high elevations. When birds were examined by habitat group, aquatic and riparian–meadow birds showed a decrease in diversity at higher elevations, but upland birds did not, as was the case for birds in lotic ecosystems (see Chapter 5). Thus, aquatic and riparian–meadow birds were responsible for the observed pattern with all birds. The negative relationship between abundance and precipitation seems contradictory given that productivity generally increases with precipitation (Rosenzweig 1995), but most likely it is an artifact of the positive relationship between precipitation and elevation. Further, precipitation in the basin falls mainly as snow at higher elevations and is therefore unlikely to increase productivity at those elevations.

Lentic units surrounded by steep slopes supported fewer species of riparian–meadow birds. This pattern is attributable to decreased meadow and riparian vegetation around those units and the close association of steep terrain with higher elevations. The steepest slopes in the basin are extremely rocky, with gradients approaching 90 degrees. Although meadows may occur on some steep slopes, they are less likely to form on rocky soils where water percolates quickly through (Ratliff 1988), and cliff-like, rocky slopes are more likely to be free of riparian vegetation because of rapid runoff and insufficient soil cover. This lack of suitable habitat on steep slopes was likely responsible for the lower richness of riparian–meadow birds.

In general, bird diversity was greatest at sample units on the east side and lowest at sample units on the west side of the basin. The north and south sides were intermediate in diversity, as expected given the intermediate nature of environmental characteristics in those basin orientations. Lentic units on the east side appear to provide some of the best habitat for aquatic and riparian–meadow birds in the basin; some east side units, such as Grass Lake at Luther Pass and Spooner Lake, are very productive, as indicated by the diversity and abundance of littoral zone plants at those sites. Many were also surrounded by meadows. These sites therefore provide quality foraging and nesting habitat for aquatic and riparian–meadow birds. The scarcity of aquatic and meadow habitat on the east side of the basin (Manley et al. 2000) may also contribute to high diversity by causing birds on the east side to congregate at a few lentic units. Upland birds, conversely, were more diverse in other basin orientations, suggesting a greater diversity of habitats for upland birds in the Sierra Nevada as compared to the Great Basin Zoogeographic Province.

The high diversity of aquatic and riparian–meadow birds on the east side highlights the importance of protecting and restoring lentic ecosystems in that basin orientation (Manley et al. 2000). Lentic ecosystems on the east side are rare and clearly can have high biological diversity. Aquatic and riparian conservation efforts in the basin could be most effective by focusing on these ecosystems first.

Potential food items for aquatic birds were poor predictors of aquatic bird diversity, with the exception of plant richness. In fact, aquatic birds were negatively related to caddisfly frequency, which was unexpected given that caddisflies are a common prey item for waterfowl (Eldridge 1990). However, caddisflies occurred least frequently on the east side of the basin, where aquatic bird diversity was highest, suggesting that factors other than caddisfly occurrence are the strongest determinants of aquatic bird occurrence. Aquatic birds also were not associated with mayflies, stoneflies, or the overall abundance of aquatic macroinvertebrates. It is possible that our sampling was not intensive enough (10 samples per sample unit may have been too few, although a wide range of macroinvertebrate abundance was represented) or we did not effectively sample the types of invertebrates aquatic birds in the basin consume.

More species were present at large sample units. Increases in species richness with increasing area have been shown for decades in many taxa (MacArthur and Wilson 1967, Ricklefs 1993), including aquatic birds (e.g., Brown and Dinsmore 1986, Baker et al. 1992, Baldassare and Bolen 1994). Part of this relationship may be attributable to a bias of increased sampling, but in addition, larger sample units are likely to encompass a wider range of habitats and therefore a larger array of species (Ricklefs 1993). Indeed, some positive relationships with sample unit area were still present when we accounted for sampling effort, showing that there were more birds *per unit area* at large sample units than at small sample units. Finally, aquatic birds were not detected at the smallest sample units. Small lentic units likely have inadequate food resources as well as a lack of suitable nesting substrate and choices of cover to support aquatic birds.

These results suggest that focusing conservation efforts on larger lentic sample units, especially ones on the east side and at lower elevations, will provide the greatest benefit to supporting the biodiversity of aquatic and riparian–meadow birds. We did not assess whether species associated with these trends were common or rare. Rare species may not be entirely accommodated by this conservation approach; additional conservation efforts may be needed. Furthermore, small lentic sample units may be important for other species, such as amphibians. All components of diversity need to be taken into account, to the extent possible, in conservation efforts.

Patterns of Amphibian Diversity

No strong predictors of amphibian species richness were evident in this study. However, richness was generally lower in deep sample units with rocky substrates and higher in sample units with silt substrates. Substrate and depth both have been shown to affect the distributions of aquatic amphibians (Zeiner et al. 1988, Hecnar and McCloskey 1997). Deep lakes and sample units with rocky substrates generally had fewer littoral zone plants, suggesting less available cover for adults and larvae and less suitable substrate for egg masses. Such sample units also had more fish, indicating potentially higher predation pressure. Neither substrate nor the presence of fish had significant effects on amphibian species richness independently, but the synergistic effects of the 2 characteristics may have resulted in reduced amphibian species richness.

Amphibian species richness commonly decreases with elevation (Duellman and Trueb 1986). We did not find this pattern. Most likely the basin represents too small an elevational gradient (roughly 1000 m) to show altitudinal variation in such a small number of amphibian species. Further, the typical elevational range of each native amphibian encompasses the basin's highest elevations (Zeiner et al. 1988), so it is not surprising that amphibians were no less diverse at higher elevations.

The values we obtained for species richness were not highly variable—only 10 sample units (11.4%) had more than 1 species—suggesting that the species richness of amphibians in species-poor environments may not be very sensitive measures of a site's productivity or ability to support biological diversity. Further, the patterns we observed for amphibian species richness mirrored those observed for Pacific treefrog occurrence and abundance (see Chapter 12), suggesting that the occurrence of treefrogs, the most common amphibian in our surveys, drove the species richness values. Species richness is a measure that does not reveal the relative contributions of common and rare species.

Patterns of Littoral Zone Plant Diversity

By far, the factor most closely associated with littoral zone plants in this study was the relative abundance of silt substrates. Plants were more common and more diverse in silt substrates than in any other substrate type, and were negatively related to all other substrate types. The pattern of lower richness and abundance of plants at high elevations that we observed might be explained by corollary substrates. Specifically, some rocky substrates, such as bedrock and boulders, were more common at high elevations, perhaps accounting for lower plant cover. The patterns we observed are similar to those reported in the literature (Goldman and Horne 1983, but see Nichols 1992) and indicate that at least some of the variation in the occurrence of aquatic plants can be described by examining geomorphologic features. In addition, the decline in plant occurrence at high elevations may result partly from the general decline in productivity with elevation that affects many taxonomic groups (Whittaker 1975, Rosenzweig 1995). Many environmental factors in extreme environments, such as temperature and the length of the growing season, may limit local distributions of plants.

Sample units surrounded by riparian and meadow vegetation supported a diversity of littoral zone plants. Two factors may underlie this relationship: comparable productivity between the terrestrial and aquatic environments, and sampling error due to the difficulty of defining the boundary of the sample unit. First, it is likely that some abiotic factors affect terrestrial and aquatic environments similarly, resulting in a concordance of productivity between the lentic body and its associated uplands. Productive ecosystems like meadows may be commonly associated with high productivity in the lentic body, manifested as increased plant diversity. Alternatively, the relationship between terrestrial vegetation and littoral zone plants may be attributable partly to the difficulty of defining the boundary of the lentic body in some cases, affecting the determination of which plants occupied the littoral zone. Meadows surrounding lakes or ponds are often inundated and willows in riparian areas may be under water, especially in the spring and early summer. Therefore, some plants that were out of the water for most of the growing season might have been determined to occupy the littoral zone, yielding increased estimates of plant diversity at sites with abundant riparian or meadow vegetation. The time of year a sample unit is visited will affect any assessment of littoral zone vegetation.

An important environmental correlate of plant occurrence may be the depth of water in the littoral zone. Aquatic macrophytes occur almost exclusively in shallow water, where the substrate is close to the water surface and light penetration is not severely reduced (Goldman and Horne 1983). Sample units with a gradual increase in depth from the littoral zone to the pelagic zone are likely to support more plants than sample units with an immediate drop-off from the shore. We did not measure this feature directly, but did observe a decrease in plant richness and frequency with increasing maximum depth. Maximum depth is likely to correlate positively with littoral zone depth, as sample units with large maximum depth were generally larger sample units with bedrock and boulders, substrates which tend to increase littoral zone depth. Still, a more accurate assessment of the effects of depth could be obtained by measuring littoral zone depth directly.

Future efforts to determine environmental relationships of littoral zone plant diversity in the basin could benefit from additional field measurements that were beyond the scope of this study. For example, various measurements of water chemistry, such as dissolved oxygen, pH, and the presence of certain ions, have been shown to affect aquatic plant species composition (Kunii 1991, Jackson and Charles 1988, Weiher and Boylen 1994, Lewis and Wang 1997).

Summary Discussion

The various measures of alpha diversity showed different patterns with environmental characteristics, although there were some similarities across groups. Relationships of diversity to environmental gradients provide a relatively clear and simple reflection of diversity patterns among groups (Table 239). Nearly every environmental gradient was associated with at least 1 alpha diversity measure. The environmental gradient most strongly related to alpha diversity overall was the elevation–precipitation gradient, along which 4 bird diversity measures and plant diversity declined. Three of the 5 bird richness measures were also most strongly associated with the elevation–precipitation gradient relative to the other gradients studied, and the elevation–precipitation gradient was second only to sample unit area in its influence on littoral zone plant diversity. Similar but weaker relationships were observed between bird species richness and the subalpine vegetation gradient, reflecting the high correlation between these two gradients. Obviously, elevation–precipitation has similar effects across at least these two taxonomic groups, and may also reflect an interrelationship between the richness of aquatic and riparian associated bird species and aquatic-associated plant species. Thus, the management of lower elevation lakes and ponds may have a great effect on the diversity of dependent bird and plant species, and also may have a significant effect on the overall diversity and abundance of aquatic and riparian associated bird species in the basin.

Sample unit area had the strongest relationship of any gradient on the overall bird diversity of a site and the littoral zone plant diversity. It is not surprising that larger sites would have the potential to provide suitable habitat for a greater diversity of species, but it does emphasize the need to consider the important contribution that larger water bodies play in supporting aquatic-associated species diversity. Given that site diversity was closely associated with abundance, these larger lakes may play an important role in supporting viable populations in the basin. It is likely that larger lakes serve as sources of individuals to populate and repopulate smaller lakes and ponds where species may be extirpated through a variety of processes. In order to say anything more definitive about their role in supporting populations of a diversity of species in the basin, we would need to investigate the reproductive success of species in larger lakes compared to smaller lakes.

The riparian vegetation gradient was positively associated with both bird and plant diversity, and appeared to be an influential factor affecting upland bird species richness. The management of riparian vegetation is most often approached with the support of aquatic and riparian obligates in mind. These results suggest that riparian vegetation plays an important role in supporting a diversity of bird and plant species across a range of habitat affiliations. Thus the management of riparian communities should consider a broad array of species objectives and potential impacts, not just aquatic and riparian obligates and associates.

Substrate gradients were associated solely and weakly with bird species richness measures; however, plant species diversity was closely associated with individual substrate variables. Patterns of association were similar for riparian–meadow birds and littoral zone plants, with both groups being more speciose in association with silty substrates and less speciose in association with rocky substrates. Silty substrates are more likely to be present at lower elevation, gently sloping sites because these conditions are generally conducive to the deposition of these lighter substrates through water and wind transport.

TABLE 239. Summary of relationships observed between with alpha diversity measures and environmental gradients associated with 88 lentic sample units in the Lake Tahoe basin. Black circles represent the strongest correlations, gray circles the next strongest, striped circles the third strongest, and open circles the fourth strongest. Only significant correlations are displayed. Correlations among aquatic plant diversity and substrate–plant gradients were not explored because littoral zone plant diversity was included in those gradients.

Gradient category	Gradient	All bird species richness	Site bird diversity	Aquatic bird species richness	Riparian–meadow bird species richness	Upland bird species richness	Amphibian species richness	Littoral zone plant diversity
Abiotic Environment	Elevation–precipitation	Black	Gray	Black	Black			Gray
	Sample unit area		Black					Black
Vegetation	Riparian vegetation	Open				Black		Striped
	Aspen to meadow vegetation			Gray				Open
	Subalpine vegetation	Gray	Striped		Striped	Gray		
Substrate–aquatic plants	Sand to silt				Open			
	Bedrock–boulders	Striped		Striped	Gray			
	Cobbles–pebbles							

No gradients were related to amphibian species richness, but a negative relationship between richness and cobbles was found. In addition, examining only gradients omits considerations such as the presence of fish, which may have been a factor influencing the richness of amphibians.

The differences in environmental relationships among taxonomic and habitat groups illustrate the challenges in maintaining and restoring lentic riparian ecosystems for multiple taxonomic groups. A similar disparity among environmental characteristics associated with alpha diversity was found in lotic riparian ecosystems (see Chapter 10). It follows that restoration efforts need to take into account the differing habitat associations of the basin's biota. For example, adding boulders to lakes or ponds to increase available cover for fish may result in unfavorable substrates for amphibians and aquatic plants. On the positive side, some management actions may accrue benefits to species that are not the focus of those actions. For instance, increasing riparian vegetation along a meadow to improve habitat for riparian birds may also increase the diversity and abundance of upland birds.

This study has highlighted some information about aquatic birds, amphibians, and littoral zone plants, which have not previously been studied in the basin in a systematic manner. The elucidation of their environmental relationships should inform restoration efforts targeted toward those species. Furthermore, the data collected serve as baseline information for future surveys. The historical focus in terms of restoration in the basin has been Lake Tahoe, but other lentic ecosystems in the basin are beginning to receive much-needed conservation and restoration attention.